Final Report:
Inventory of Invertebrate Fauna in Devils Postpile National Monument

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Summary

The Sierra Nevada Ecosystem Project identified aquatic and riparian systems as the most altered and impaired habitats of the Sierra Nevada range. Devils Postpile National Monument includes many kilometers of high-elevation stream habitat and associated meadow habitat, dominated by the Middle Fork of the San Joaquin River. This environment is under significant pressure from intense usage. Although there has been little inventory of invertebrates in Devils Postpile, these fauna are an important group to survey because of the variety of ecosystem services that they provide. Invertebrates include primary, secondary, tertiary, and higher-level consumers, and in turn invertebrates are a critical food resource for a variety of terrestrial, aquatic, and flying species.

This inventory investigated fauna throughout the riparian corridor of the Middle Fork of the San Joaquin River. We sampled riffle and pool habitats in the river and both flooded and dry portions of meadows. We chose quantitative sampling devices for use in this inventory so that we could also report baseline ecological data.

Sampling was performed over two growing seasons, from May 2003 through October 2004, from snowmelt until snowfall, and we have also included limited data collected before the start of the project, during the summer of 2002. We sampled flooded meadow habitat with a throw trap which is a

quantitative device for sampling still, shallow water with submerged and/or emergent vegetation. We sampled terrestrial habitat with a vacuum net apparatus. As we sought a method as efficient across a wide range of fauna as throw trapping, we tested the efficiency of the vacuum net in two different ways. Despite the efficiency of the vacuum netting technique, there are concerns about using this protocol in wilderness areas, because the vacuum is a mechanized device. Pitfall trapping is a possible non-mechanized alternatives to vacuum netting. We were able to add a comparison of the assemblage characterization provided by vacuum netting versus that determined by pitfall trapping at no cost to NPS (National Science Foundation funding). We used Surber sampling for riffles and substrate sampling for pools in an effort to complement previous kick-net sampling in the San Joaquin and to provide density data on assemblages. The Surber sampler targets small organisms that use cobble beds in shallow riffle habitats. We sampled pools with basket substrate samplers that make use of materials found on the river bottom; these materials are enclosed in a wire basket and sunk into the sediment and cobbles such that the top of the basket was level with the substrate.

Surber samplers, substrate samplers, throw trapping and vacuum netting all produced quantitative density data. Pitfall trapping remains an alternative for terrestrial sampling but did not sample flying fauna and provided only catch-per-unit-effort data and is also disruptive to meadow habitat. Sweep netting and baiting may be better alternatives for non-mechanized sampling in meadows.

We documented 77 taxa from dry meadow habitat, 29 from flooded meadow habitat, and 51 from the San Joaquin River. The 77 taxa from dry meadow habitat represented eleven orders and 50 families, the highest diversity overall. In contrast, the 29 taxa from flooded meadow habitat were from six orders and fifteen families, and the 51 taxa from the river represented six orders and 27 families. Virtually all taxa from the meadows were new records for the Monument. About 40% of the river fauna were new records for Devils Postpile. Family richness was high for Diptera (flies and relatives) across all three habitats. In addition, family richness was high within the Coleoptera (beetles), Hymenoptera (wasps, ants), and Araneae (spiders) in the dry meadow and within Ephemeroptera (mayflies), Trichoptera (caddisflies), and Plecoptera (stoneflies) in the river.

Groups for which richness was high at the genus level varied among the three habitats. In the dry meadow, richness was greatest in the Cicadellidae and Delphacidae (two families of leafhoppers), the Formicidae (ants, in the order Hymenoptera), and the Chloropidae (a dipteran family). In the flooded meadow, Dytiscidae (predaceous diving beetles), Hydrophilidae (water scavenger beetles), and Culicidae (mosquitoes, Diptera) had the highest richness. In the river, we found the greatest richness in Ephemerellidae (a family of mayflies) and Chironomidae (a gnat family, Diptera).

Wet meadow habitat and riffles each harbored about 800 animals per square meter, versus about 200 per square meter in the dry meadow habitat. The substrate samplers yielded a striking 87,000 animals per cubic meter. Pools and other low-flow habitats appear to represent a significant resource. Both meadow and river fauna demonstrated a relatively high level of dominance. Diptera were abundant in all examined Devils Postpile habitats. There were greater numbers of meadow fauna present in early season than in late season. It is possible that invertebrate assemblages are even more sensitive than flora to grazing impacts in early season but more resistant to disturbance in late season. In contrast, riffle abundances were about twice as abundant in late season as in early season.

Diversity in Postpile dry meadow habitat was relatively high and similar to analogous habitat in Tuolumne Meadows. Given the ephemeral nature of the flooded meadow habitat, diversity lower than that of dry meadow habitat is not surprising. Diptera, Ephemeroptera, Coleoptera, Trichoptera, Odonata, and Hemiptera (true bugs) were collected in both Devils Postpile and Tuolumne flooded habitat, but Plecoptera (stoneflies), and Collembola (springtails) were found in Tuolumne but not in the Postpile. Although 40% of the river arthropods were new records, the river fauna was generally similar to that described by previous work in the San Joaquin, particularly at the family level.

Densities for Devils Postpile meadow fauna were essentially similar to those observed in Tuolumne, although numbers in both wet and dry samples were somewhat lower in the Postpile. Our work suggests that there are aquatic/terrestrial linkages both within meadows and with other habitats. In contrast to the results from the meadows, the greatest abundance of river fauna occurred in late season.

The more heavily used east meadow had many fewer fauna in flooded meadow habitat than were found in the west meadow. There were not pronounced differences in overall abundances in dry meadow habitat abundances between the two meadows. The lower number of fauna present in flooded habitat in the east meadow may be a function of use history, natural hydrologic regime, or both.

Introduction

The Sierra Nevada Ecosystem Project (1996) identified aquatic and riparian systems as the most altered and impaired habitats of the Sierra Nevada range. This landscape has been impacted by numerous anthropogenic stressors, including hydrologic modification (dams, diversions), logging, livestock grazing, human trampling and social trailing, mining, road building, exotic species, recreational and urban development, pesticide use in nearby agricultural lands, and climate change. Invertebrates have been particularly impacted by trail use, trampling, packstock grazing, and introduced trout, and long-term monitoring of this group is desirable in order to detect significant changes in assemblages and assist resource managers in mitigating the impacts of stressors. However, invertebrates have been largely ignored by historical inventory and monitoring programs throughout the NPS and by land managers in general; Clark and May (2002) demonstrated that vertebrates are grossly overrepresented in conservation and management efforts, whereas invertebrates are poorly represented in such programs. Although pilot surveys suggest a wealth of invertebrate biodiversity in the Sierra Nevada Ecosystem (Kimsey and Cranston. 2002, Holmquist and Schmidt-Gengenbach 2005), there is much to learn about assemblage composition, seasonality, microhabitat use, variability, or response of invertebrate populations to disturbance.

Devils Postpile National Monument includes many kilometers of high-elevation stream habitat, including the Middle Fork of the San Joaquin River. These habitats harbor high proportions of endemic taxa in insect groups such as the stoneflies and caddisflies and typically contain invertebrate assemblages composed of dozens of species with diverse roles in food webs, thus representing a significant resource. Chief among inventory needs is a thorough knowledge of the invertebrate assemblage. The Sierra Nevada Network Plan identified invertebrate inventory as a critical need (USDI 2001), and aquatic invertebrates were given a “highest priority” ranking among potential vital signs for Devils Postpile (USDI 2002a), yet an inventory has not been completed. Terrestrial invertebrates are even more poorly known throughout the Sierra Nevada ecosystem. There has been no inventory of terrestrial invertebrates in Yosemite National Park, although the need is acknowledged (USDI 2002b), or in Devils Postpile, and there has only been a pilot project in Sequoia and Kings Canyon National Parks (Kimsey and Cranston 2002). In summary, invertebrates are known to be critically important to ecosystem function, but remain poorly understood in Devils Postpile and throughout the Sierra Nevada Network.

Invertebrates are a good target group for inventory, because this group includes primary, secondary, tertiary, and higher-level consumers, and in turn invertebrates are a critical food resource for a variety of terrestrial, aquatic, and flying species. Assessment of trail and grazing disturbances in Yosemite suggests that these impacts cascade through the invertebrate food web (Holmquist 2004; Holmquist & Schmidt-Gengenbach 2002), and invertebrates have been shown to be similarly sensitive to recreation impacts in other systems (Eckrich & Holmquist 2000, Uhrin & Holmquist, 2003, Holmquist and Schmidt-Gengenbach 2005). Thus, a baseline survey of invertebrates is valuable for assessment of future disturbances and should be a useful contribution to the Sierra Nevada Ecosystem database.

This survey investigated fauna throughout the riparian corridor of the Middle Fork of the San Joaquin River and adjacent meadows. We sampled riffle and pool habitats in the river and both flooded and dry portions of meadows. We chose quantitative sampling devices for use in this inventory so that we could also report baseline ecological data and trends in space and time.

Methods

Sampling was performed over two growing seasons, from May 2003 through October 2004, from snowmelt until snowfall (Fig 1). We have also included limited data collected before the start of the project, during the summer of 2002. Meadow sampling included both wet (early season, aquatic and pond-like) and dry (mid- and late-season, terrestrial) phases (Fig 1). Both aquatic and terrestrial sampling was performed such that as much spatial and temporal variability as possible was included in the inventory. To this end samples were evenly allocated among months but were randomly allocated to individual days throughout the season and to individual hours within sampling days. Aquatic samples were randomly allocated throughout the river reach (Fig 2, Table 1). Meadow samples were divided between the east (historically more impacted by trampling and trailing and also dryer) meadow and west (relatively pristine and wetter) meadow. Samples within meadows were allocated randomly.

Aquatic meadow fauna. We sampled flooded meadow habitat with a throw trap (Fig. 3) which is a quantitative device for sampling still, shallow water with submerged and/or emergent vegetation (Kushlan 1981, Holmquist et al., 1989). The throw trap (or drop trap) is a box lacking a solid top or bottom that is cleared of fauna with a net. The trap has been shown to be highly efficient, relative to other collecting devices, for quantitatively sampling fauna in vegetated aquatic habitats (Kushlan 1981, Jacobsen & Kushlan 1987, Rozas & Minello 1997). Throw trapping of well-separated stations is effectively sampling with replacement (Jacobsen & Kushlan 1987), and re-sampling vegetated sites at six month intervals over a period of four years does not cause shifts in measures of vegetation cover or assemblages of mobile fauna (J.G. Holmquist, pers. obs.). Throw traps have been used in a number of habitats including freshwater marshes (Erwin et al. 1985, Jordan et al. 1994, Ruetz et al. 2005), shallow seagrass beds (Holmquist et al. 1989), seagrass several meters below the surface (Holmquist 1997), flooded Mojave playas (Brostoff et al. submitted), and in flooded subalpine meadows in the Sierra (Holmquist and Schmidt-Gengenbach 2005).

We used a device and protocol derived from that of Kushlan (1981) and Holmquist et al. (1989). The trap was a 0.75 m x 0.75 m box without a top or bottom and constructed of sheet aluminum. The clearing device was a 0.75 m-wide framed and handled net (bar seine) with 0.5 mm square mesh. The trap was thrown downwind (Fig 3) and then pressed into the sediment. The bar seine was passed repeatedly through the trap (Fig 4) for a minimum of ten passes and until three successive passes produced no additional animals. The bar seine was washed in a tub until free of fauna after each pass (Fig 4). We then sorted fauna live, on site (Fig 4). Live sorting aids in discriminating animals from detritus and other material. Large samples were subsampled with a plankton splitter (Fig 4).

Terrestrial meadow fauna. We sampled terrestrial habitat with a vacuum net apparatus (Fig 5). Vacuums with nets inserted in the intake tube generally offer an improvement in efficiency over other methods of sampling invertebrates in vegetation, and this technique has been used in a variety of studies (e.g., Richmond and Graham 1969, Hand 1986, Macleod et al. 1994). Vacuums are more efficient than visual censuses (Arnold et al. 1973) or sweep netting (e.g., Dietrick et al. 1960, Arnold et al. 1973, Buffington and Redak 1998), especially for ground dwellers (New 1998), because sweep netting underestimates ground-dwelling invertebrates (Whittaker 1952, Hughes 1955). This increased efficiency incorporates both abundance and species richness (Buffington and Redak 1998). Vacuums also cause less damage to invertebrates than sweep netting (Callahan et al. 1966) and are particularly efficient at removing animals in litter and lower vegetation (Stewart and Wright 1995). Vacuum sampling has been found to be most efficient when used with some form of enclosure box which is placed prior to suctioning (Henderson and

Whittaker 1977, Hower and Ferguson 1972, Harper and Guynn 1998), although enclosures are often not used.

Despite the general efficiency of vacuum sampling, this method has not worked well in capturing rapidly-moving insects (Powell et al. 1996). The operator creates disturbance, and even if an enclosure box is used, flying and other vagile insects will flee the area before the enclosure is placed. Much of the efficiency of throw trapping is a function of the “throwing,” i.e., by tossing the trap from a distance, animals are captured before the field personnel are detected by the fauna. In an effort to create a terrestrial analog to the throw trap, Holmquist and Schmidt-Gengenbach (2002), constructed a 0.5 m^2 steel quadrat with a conical mesh covering (Fig 5). The mesh cone has an elasticized hole at the apex through which a vacuum intake tube can be inserted. This quadrat is thrown toward the target area from a distance and staked in place to form a seal with the substrate. The vacuum intake is then inserted through the mesh aperture for sampling (Fig 5).

We used a Craftsman 320 km/h gasoline vacuum modified with a mesh collecting chamber inserted in the intake tube in conjunction with the netted quadrat (Fig 5). Henderson and Whittaker (1977) and Hossain et al. (1999) found that vacuum sampling is most efficient if initial vacuum passes are made and then followed by clipping of vegetation and additional vacuuming. After staking the quadrat, we made multiple passes through the vegetation with the vacuum intake from different orientations over a two-minute period. Then the intake was removed, and the vegetation was clipped with trimmers inserted through the elasticized aperture of the netted quadrat. The trimmers were then removed and the intake inserted for an additional two minutes of sampling. The intake was then extracted from the quadrat, the integral mesh collecting bag was removed from the intake tube, and the fauna and litter were transferred to a bag and placed on ice. Sorting was done at the laboratory.

Vacuum net efficiency. As we sought a method as efficient across a wide range of fauna as throw trapping, we tested the efficiency of the method in two different ways. 1) We released known numbers of both flying and non-flying insects into a previously-placed netted quadrat in order to test vacuuming efficiency. 2) We assessed the contribution of the thrown netted quadrat by sampling a naturally occurring assemblage with and without the netted quadrat.

In the first test, we used crickets, *Acheta domesticus,* and ants, *Formica argentea*, as our subject organisms. The animals were released into the netted quadrats and given a settling period as recommended by Hossain et al. (1999) before sampling using our protocol. Fifteen crickets and 25 ants were released into each of four netted quadrats.

In the second test, we assessed the usefulness of the thrown netted quadrat by completing 14 pairs of net/no-net samples using our netted quadrat and a non-netted quadrat. The netted and unnetted quadrats were thrown into the same vegetated habitat and sampled with the vacuum.

Comparisons with pitfall trapping. Despite the efficiency of the vacuum netting technique, there are concerns about using this protocol in wilderness areas, because the vacuum is a mechanized device. Pitfall traps, sweep netting, and baiting are possible non-mechanized alternatives to vacuum netting. We were able to add a comparison of the assemblage characterization provided by vacuum netting versus that determined by pitfall trapping at no cost to NPS (National Science Foundation funding).

We established eight replicate matrices of pitfall traps in Devils Postpile. Each replicate included fifteen individual traps arranged in three rows and five columns with a 1m spacing. Pitfall traps consisted of clear plastic cups, 7.6 cm in diameter and 7.6 cm deep. The cups were placed in holes of the same dimensions, excavated with a hand trowel, so that the lip of the plastic container was level with the ground. The cores of soil and plant matter from the holes were placed in an area protected from sun and wind. At the conclusion of the study each soil core was returned to its original site.

Pilot studies indicated greater capture during daylight than at night, so we set the 120 traps on thirteen different days in July and August of 2004. A six-hour sampling period was used for each of these trap sets. After six hours all captured fauna were identified to order and released.

River sampling. We used Surber sampling for riffles and substrate sampling for pools in an effort to complement Rowan and Parmenter's (1994) kick-net sampling in the San Joaquin and to provide density data on assemblages. Both of our methods sample a smaller area but do so more intensively.

The Surber sampler (Surber 1937, Hauer and Resh 1986; Fig 6) targets small organisms that use cobble beds in shallow riffle habitats. The sampler was a 0.3 m x 0.3 m framed net that demarcates a section of the river bed; the associated substrate was disturbed manually, and organisms were swept downstream into the net, providing a relatively quantitative sample. Each sample was sorted live.

We sampled pools with basket substrate samplers (Mason et al. 1967, Merritt et al. 1996) that make use of materials found on the river bottom; these materials are enclosed in a wire basket and sunk into the sediment and cobbles such that the top of the basket was level with the substrate (Fig 7). The hardware cloth baskets were 36 cm in length, 16 cm in width, and 12.5 cm in height and had a square mesh size of 12 mm. The baskets were left in place to allow colonization and siltation and were raised after one year. This method does not depend on flow and thus is ideal for relatively quiescent pools. Substrate samplers are also quantitative and provide population densities per unit volume of substrate. The samplers became so integrated into the surrounding substrate that some searching was required to locate the baskets. Samples were sorted live; large samples were subsampled with the plankton splitter (Fig 4).

Taxa were identified to the lowest taxonomic level possible with available literature. We have attempted to be conservative in indicating our degree of certainty on identifications.

Results

Vacuum net efficiency. In the test in which fauna were released into the netted quadrat, cricket recapture was 100% (SE= 0%, n=4), and ant recapture was 92% (SE= 2.8%, n= 4).

More fauna were collected in the net samples than in the no-net samples (mean= 125 versus 107 individuals/m^2; SE= 35.7 and 42.7, respectively; Fig. 8), but this difference was not significant (one-tailed paired t-test, p= 0.12). Differences were greater, and significant, when volant (flying) individuals were considered in isolation (mean net= 54.0 individuals/m^2, SE= 12.1; mean no-net= 24.4, SE= 6.65; p=0.00039; Fig. 8). Similarly, total species richness did not differ (mean net= 12.7 species/0.25m^2, SE= 1.13; mean no-net= 11.4, SE= 1.16; p=0.10; Fig. 9), but volant species richness was significantly greater in the netted quadrats than in the non-netted quadrats (mean net= 5.86 species/0.25m^2, SE= 0.417; mean no-net= 4.79, SE= 0.505; p=0.030; Fig. 9).

Comparisons of assemblage structure revealed by vacuum netting and pitfall trapping was necessarily by percentage composition (Fig. 10), because pitfall traps do not provide faunal densities. Pitfall traps failed to collect flying fauna, including the two dominant taxa, Diptera (flies) and Homoptera (leafhoppers). Pitfall trap samples were instead dominated by Hymenoptera (ants), Acari (mites), and Araneae (spiders).

Survey. We documented 77 taxa from dry meadow habitat (Table 2), 29 from flooded meadow habitat (Table 3), and 51 from the San Joaquin River (Table 4). Virtually all taxa from the meadows were new records for the Monument. About 40% of the river fauna were new records (see also Rowan and Parmenter 1994). None of the taxa collected were sensitive species. We collected one exotic species, the leafhopper *Exitianus exitiosus.*

The 77 taxa from dry meadow habitat represented eleven orders and 50 families, the highest diversity overall. In contrast, the 29 taxa from flooded meadow habitat were from six orders and fifteen families, and the 51 taxa from the river represented six orders and 27 families.

Family richness was high for Diptera (flies and relatives) across all three habitats (Tables 2,3,4). In addition, family richness was high within the Coleoptera (beetles), Hymenoptera (wasps, ants), and Araneae (spiders) in the dry meadow and within Ephemeroptera (mayflies), Trichoptera (caddisflies), and Plecoptera (stoneflies) in the river.

Groups for which richness was high at the genus level varied among the three habitats. In the dry meadow, richness was greatest in the Cicadellidae and Delphacidae (two families of Homoptera, or leafhoppers), in the Formicidae (ants, in the order Hymenoptera), and in the Chloropidae (a dipteran family; Table 2). In the flooded meadow, Dytiscidae (predaceous diving beetles), Hydrophilidae (water scavenger beetles), and Culicidae (mosquitoes, Diptera) had the highest richness (Table 3). In the river, we found the greatest richness in Ephemerellidae (a family of mayflies) and Chironomidae (a gnat family, Diptera; Table 4).

Faunal assemblage structure. There were substantial differences in abundance among the sampled habitats (Figs 11-14). Wet meadow habitat and riffles each harbored about 800 animals per square meter, versus about 200 per square meter in dry meadow habitat. The substrate samplers yielded a striking 87,000 animals per cubic meter.

Both meadow and river fauna demonstrated a relatively high level of dominance (Figs 11-14). Dry meadows and pools had somewhat more evenness than the flooded meadows and riffles.

Diptera were important in all examined DEPO habitats. Dry meadows were dominated by Diptera and Homoptera (Fig 11), whereas the flooded meadows were dominated by Diptera and Ephemeroptera (Fig 12). Ephemeroptera were dominant in the riffles, followed by Trichoptera and Diptera (Fig 13), and Diptera and Ephemeroptera were the most abundant taxa in the pools (Fig 14). The greatest dominance at the genus and family levels occurred in the flooded meadows, where *Aedes* (Culicidae, mosquitoes) accounted for most of the dipteran abundance, and *Siphlonurus* (Siphlonuridae) was the only mayfly present. These two genera represented 80% of the individuals collected in the flooded meadows.

There were greater numbers of meadow fauna present in early season than in late season. Abundances of fauna were almost four times greater in flooded habitat (present only during the first month after meltoff; fig 12) than in early-season dry meadow habitat (Figs 11, 15, 16). Total dry abundances dropped in late season, to about one-sixth and one-third the abundances present in early season samples in the east and west meadows, respectively (Figs 15, 16). This seasonal trend was consistent across taxa (sign test; $p < 0.0005$). The reduction in abundances was greater in the east meadow than the west meadow across taxa, despite the differing contributions to total abundance by the various taxa in the two meadows (Figs 15, 16; sign test; $p < 0.05$).

In contrast, riffle fauna were about twice as abundant in late season as in early season (Fig 17). These trends were consistent across all fauna (sign test; $p < 0.025$).

There were no clear long-term trends in total abundances over three years of meadow sampling, either for wet (Fig 18) or dry (Fig 19) habitat.

Riffle abundances fell during the study from 1172 animals per square meter (SE= 556) to 443 (SE= 77).

Discussion

Vacuum net efficiency. The thrown netted quadrat appeared to more efficiently capture flying insects and, in conjunction with the vacuum, resulted in a technique for sampling alpine meadows that was analogous to the throw trap in quantitative efficiency. The result is a technique that yields densities rather than catch-per-unit-effort data.

The utility of the vacuum net in capturing flying taxa and producing density data stood in contrast to the results obtained for the pitfall traps in DEPO. However, the ground-dwelling fauna, such as ants and ground beetles, that were effectively sampled are arguably very useful vital signs (ants: Greenslade 1978, Andersen 1990, Alonso 2000, Andersen and Majer 2004; ground beetles: Stork 1990, Freitag 1979, Pearson and Cassola 1992). Pitfall traps necessarily yield only catch-per-unit-effort data instead of densities, but these traps, perhaps in conjunction with sweep netting, are a viable sampling alternative if vacuum use proves intractable due to wilderness considerations. We are currently comparing results obtained by vacuum netting versus sweep netting in Yosemite and Sequoia/Kings Canyon National Parks. Our initial results suggest that sweep netting, though collecting primarily flying fauna and virtually incapable of yielding density data, does represent a simple and rapid collection technique. In addition, sweep netting appears to be a more viable collection method in areas that are saturated with water but not inundated, i.e., too dry for throw trapping and too wet for vacuum netting. Baiting (Bestelmeyer et al. 2000, Delabie et al. 2000) is another option if ants were to be targeted as vital signs (Alonso 2000, Andersen and Majer 2004).

Survey. Diversity in DEPO dry meadow habitat was similar to analogous habitat in Tuolumne Meadows (Holmquist and Schmidt-Gengenbach 2005), which produced nine orders and 55 families during 2004 sampling using the same techniques as in the current study. The same orders were represented in both Tuolumne Meadows and Devils Postpile, but in addition, Isoptera (termites) and Odonata (damsel and dragonflies) were collected in the Postpile. Ants, though present, were much less important in DEPO than in Yosemite, possibly because of differences in soil moisture. There was greater sampling intensity in Tuolumne, but the Postpile sampling was conducted over a longer period of time. Most of the same families were found in both locations for the majority of orders, but there was only about a 50% overlap in fly and spider families. These differences would probably wane with increased sampling in both locations. It will be informative to compare the faunas again after our planned 2005 Tuolumne sampling.

Both Tolbert et al. (1977), working in Colorado tundra, and Dethier (1984), working in Swiss alpine meadows noted an inordinate number of predators in their systems, and our Yosemite and Devil's Postpile results also show a relatively "top-heavy" trophic structure. The large number of spiders and other predators may be taking advantage of the many transient species that emerge from aquatic habitats.

Given the ephemeral nature of the flooded meadow habitat, lower diversity is not surprising. For instance, *Siphlonurus* (Siphlonuridae) may be the only mayfly family capable of rapidly exploiting these ponds, and siphlonurids were also the only mayflies collected in flooded Tuolumne meadows (Holmquist and Schmidt-Gengenbach 2005). Similarly, limnephilids were the only caddisflies collected in both the Postpile and at Tuolumne. Our initial samples in wetter montane meadows in Sequoia/Kings Canyon National Parks indicate that siphlonurids are also likely to be the most common mayflies in that system. However, some Heptageniidae were also present at Sequoia/Kings, likely as a function of the greater stream influence and associated sheet flow in these wetter meadows.

Diptera, Ephemeroptera, Coleoptera, Trichoptera, Odonata, and Hemiptera (true bugs) were collected in both DEPO and Tuolumne (Holmquist and Schmidt-Gengenbach 2005) flooded habitat, but Plecoptera (stoneflies), and Collembola (springtails) were found in Tuolumne but not in the Postpile. There was about the same level of family similarity between the two sampling areas as for the dry meadow samples. Interestingly, one of our first throw trap samples in our current Sequoia/Kings Canyon National Park sampling was dominated by stoneflies, perhaps again a function of prominent sheet flow.

Although 40% of the river arthropods were new records, the river fauna was very similar to that described by Rowan and Parmenter (1994), particularly at the family level. Both studies collected similar numbers of families and individual taxa. Rowan and Parmenter did collect an order that we did not: Megaloptera. Different methods were used, as planned in the design of this project. Rowan and Parmenter used kick sampling, an excellent technique for rapidly characterizing a faunal assemblage. We used Surber sampling for riffles and substrate sampling for pools in an effort to complement Rowan and Parmenter's earlier work and to provide density data on assemblages. Both of the methods used in our study sample a smaller area but do so more intensively. Nonetheless, these two surveys, separated by ten years, show equal to or greater similarity for river fauna than were found for flooded and dry meadow fauna in the Postpile (current study) versus Tuolumne (Holmquist and Schmidt-Gengenbach 2005).

One introduced species has appeared in our meadow samples to date. We have collected the leafhopper *Exitianus exitiosus* from both Tuolumne Meadows (Holmquist and Schmidt-Gengenbach 2005) and DEPO. Among the many introduced species that may use meadows in the Sierra are the Diamondback Moth *Plutella xyllostella* and Africanized Honeybees, *Apis mellifera scutellata*. The latter have not been collected in Network Parks to our knowledge but lower elevations are within the current expected range for the bees. Other potential invasives of note include the Argentine Ant (*Iridomyrmex humilis*) and Red Imported Fire Ant (*Solenopsis wagneri* (*invicta*)) which are probably already present, or soon to arrive, within the Network at lower elevations. We have a reliable May 2005 report of an encounter with "red, stinging ants" found in potting soil in Three Rivers, and these ants were likely *Solenopsis wagneri* (*invicta*).

Faunal assemblage structure. Densities for DEPO meadow fauna were generally similar to those observed in Tuolumne (Holmquist and Schmidt-Gengenbach 2005), although numbers in both wet and dry samples were somewhat lower at DEPO. Other trends were similar as well. There were many more fauna present in early season than in late season. In both DEPO and Tuolumne, beetles showed substantial decreases through the season, whereas spiders were among the taxa that declined the least through the growing season in both studies. Flooded habitat produced large numbers of animals; wet samples had about five times the abundance of dry samples during early season.

Our work suggests that there are aquatic/terrestrial linkages both within meadows and with other habitats. Meadows are flooded during the first four weeks after snowmelt. During this time, the meadows are pond-like with emergent vegetation or slough-like with slow drainage into the nearby river and streamlets. Thus, in the wet phase, meadows are miniatures of Marjorie Stoneman Douglas' (1947) "River of Grass," also known as the Everglades. The meadows are similarly teeming with life, and the mud and water appear alive with wriggling larvae, up to 1,000 or more per square meter. Our study suggests that much of the annual arthropod production in Devil's Postpile meadows occurs in the flooded portions during this short time period. Many of these insects spend their adult lives in the neighboring dry portions of meadows before returning to wet meadow habitat for egg laying. However, for many taxa, there are several orders of magnitude more aquatic larvae found in flooded habitat than adults found in dry meadow habitat. Although some losses are undoubtedly due to aquatic predation, this disparity suggests that many of the insects emerging from the wet-phase meadows are transported into neighboring upland forests and thus fuel the food webs in these other habitats.

Meadows may thus be a nexus for exchanges with streams and forests in addition to the aquatic-terrestrial linkages that are internal to the meadow system.

Early-season meadow habitat is known to be susceptible to grazing impacts, and management decisions are made with this sensitivity in mind. Given that invertebrate production appeared to be very high in early season and very low in late season, it is possible that invertebrate assemblages are even more sensitive than flora to grazing impacts in early season but more resistant to disturbance in late season. The observed negative influence of soil compaction on meadow invertebrates (Holmquist and Schmidt-Gengenbach 2005) suggests that soil compaction from stock trampling could negatively affect meadow invertebrates as well as vegetation. The importance of invertebrates in ecosystem function and the observed high rates of production in early-season meadows should warrant consideration when adopting meadow management practices.

There may be general altitudinal trends in meadow arthropod abundance and species richness in the Sierra. Low elevation Yosemite Valley (1,220m) dry meadow sites had 2.5 times the overall abundance of high elevation Tuolumne (2,650-3,000m) sites (227 versus 91 animals/m^2) in Yosemite NP (Holmquist and Schmidt-Gengenbach 2004; Holmquist and Schmidt-Gengenbach 2005).

Devil's Postpile NM, at an intermediate elevation of 2,300m, had intermediate abundances, with 163 arthropods/m^2. Of course, other factors, related to elevation, are likely to explain part of this trend.

The substrate samplers produced very high abundances relative to the Surber samplers. Even after conservatively correcting for depth sampled, the substrate samplers collected over 50 times the abundance of the Surber samplers. The large number of animals collected by the substrate samplers may be a function of the sampling method, the more quiescent water in which the devices were placed, and/or the greater percentage of fines and organics found in these locations. These low-flow habitats clearly represent a significant resource.

In contrast to the results from the meadows, the greatest abundance of river fauna occurred in late season. This pattern has been observed in other western lotic systems (e.g., Minshall 1981, Leland et al. 1986). Early-season streambed scouring can remove habitat and fauna, and conversely the low flows found in late season allow accumulation of fines and organics and generally provide a more benign environment for fauna, particularly early instars (Leland et al. 1986).

The more heavily used east meadow had many fewer fauna in flooded meadow habitat than were found in the west meadow. There were not pronounced differences in overall abundances in dry meadow habitat abundances between the two meadows. However, late season abundances for dry meadow habitat were lower in the east meadow than in the west meadow. The east meadow was dryer than the west meadow, and flooded portions disappeared one to three weeks earlier. Whether the dryer state of the east meadow is due to soil compaction and loss of soil moisture from years of trampling and social trailing remains unknown. These trends may be a function of use history, the natural hydrologic regime, or both.

Foot trails in alpine meadows, though less intrusive than roads, can have surprisingly large effects on invertebrates. Fragmentation of meadow plant assemblages by trails is relatively apparent, but effects on mobile fauna are more difficult to discern. Holmquist and Schmidt-Gengenbach (2004) sampled meadow invertebrate fauna in Yosemite NP using transects that ran perpendicular to trails in order to assess functional fragmentation of the meadow assemblage. Effects of trails extended further into the surrounding meadow habitat than would have been predicted on the basis of vegetation alone. Invertebrate assemblages in portions of meadows bordering trails had 24% of the abundance of "core" meadow areas across all species. Ants provide a good example of the extension of trail effects into intact meadow vegetation. There was an average of 1.6 ants per square meter in trails, and 5.0, 9.0, and

63.6 ants per square meter in vegetation next to trails, 2 meters from trails, and 5-10 meters from trails, respectively. Abundances on the trails were even lower than expected: there was a mean of only 10.2 invertebrates (of all types) per m^2 of trail versus 157.5 animals/m^2 of core meadow habitat. As seen above, meadow invertebrates are tightly-linked to both aquatic and upland forest systems, and impacts to meadow fauna can be expected to cascade into these other habitats.

Human and other diffuse trampling of non-trail substrata can also affect invertebrate fauna, although comparatively little is known in comparison to effects on vegetation (Bayfield 1979, Cole 1995a, b). Invertebrates in alpine meadow soil in Austria are negatively influenced by trampling (Meyer 1993). Abundance and species richness of soil fauna have been reduced in other systems due to soil compaction (Chappell et al. 1971; Dózsa-Farkas 1987), and this relationship has been shown to hold for meadow invertebrates as well (Holmquist and Schmidt-Gengenbach 2005). Trampling effects on mobile invertebrates in the aquatic environment can also be mediated by substrate modification (Eckrich and Holmquist 2000). Effects of heavy foot traffic on mobile terrestrial invertebrates have seen little attention, and such impacts are likely to be significant in heavily-used national parks and monuments such as Sequoia & Kings Canyon NP, Yosemite NP, and Devil’s Postpile NM, particularly in high elevation meadows with short growing seasons. A controlled experimental study would be easy to implement.

There was a great deal of year-to-year variability in both wet and dry meadow abundances, but sample sizes were low, as this study's primary goal was to maximize dispersion of sampling effort across habitats, space, and time in an effort to survey as much fauna as possible in a short period of time. Changes in community structure as a function of ongoing restoration efforts was not apparent.

Similarly, the two years of riffle sampling produced very different abundances. Nearby Convict Creek also demonstrates major inter-annual variability (Leland et al. 1986).

Although there is significant year-to-year variability in this dynamic river-meadow system, there is also considerable predictability. There are apparent trends in assemblage structure as a function of season, elevation, and habitat that have been found throughout the systems sampled to date, including DEPO, Tuolumne, Yosemite Valley, and Sequoia/Kings.

Monitoring Recommendations

Aquatic macroinvertebrates are widely accepted as important monitoring tools (Samways 1994), including the detection of early effects of climate change (Elliott 1991). Ideally, both ecological and physiological data should be available for targeted aquatic species (Elliott 1991).

Terrestrial invertebrates have received less attention, at least in the United States, as monitoring tools; cultural bias may explain some of this discrepancy. Numerous ecologists have argued against monitoring terrestrial reserves exclusively via plants and vertebrates, and have contended that invertebrates should play an important role as reserve selection criteria and as indicators because of the prominent role that these organisms play in ecosystem function (Refseth 1980, Disney 1986, Usher 1986, Majer 1987, Yen 1987, Eyre and Rushton 1989, Sutton and Collins 1991, Pearson and Cassola 1992, Usher 1992, Kremen et al. 1993, New 1993, Oliver and Beattie 1994). Plant data, though critically important, cannot serve as a proxy for invertebrate assemblage health. For instance, Kremen (1992) found little concurrence between plant richness and butterfly richness along old trail and road edges. Similarly, Holmquist and Schmidt-Gengenbach (2004) found many fewer invertebrates in disrupted portions of meadows than in core meadow habitat, despite similar vegetation parameters throughout. Erhardt and Thomas (1991) found insects to be many times more sensitive to environmental change than their host plants. Similar results have been reported from aquatic systems, e.g., Eckrich and Holmquist (2000) and Uhrin and Holmquist (2003).

Clark and May (2002), in a recent *Science* article, *Taxonomic bias in conservation research*, demonstrated that vertebrates are grossly over-represented in conservation and management efforts, whereas invertebrates are poorly represented in such programs. Insects are particularly useful as vital signs because of their abundance, species richness, ubiquitous presence, importance in ecosystem function (Holloway 1980, Rosenberg et al. 1986) and are particularly sensitive to disturbance, expressed both by mortality and emigration. Effects are often amplified by insects' prodigious reproductive potential. Also, the variety of trophic levels represented, even within a given taxon, makes for great indicator sensitivity (Samways 1994). For these reasons, invertebrates will often be better as rapid response "sentinel species" (New 1995) than vegetation surveyed in isolation.

Because of this utility, invertebrates have been used as indicators throughout the world; a few examples follow. Given the diversity present in neotropical forests, it is not surprising that insects have served as indicators in this system (Brown 1997). Europe has a long history of interest in landscape configuration, and moths, ants, and ground beetles (Carabidae) have been used as indicators of land use change (Eyre et al. 1986, Eyre and Luff 1990, Rushton et al. 1990, Erhardt and Thomas 1991, Luff and Woiwod 1995). Insects have also been used as indicators in evaluating grazing pressure in Germany (Meyer and Hans-Dieter 1996). In Australia, indicators have included grasshopper diversity in Kakadu National Park (Andersen et al. 2001) and leaf litter invertebrates in Barrine National Park (Jansen 1997). Use of invertebrates as indicators in Africa includes dung beetles in a savanna ecosystem in Tembe Elephant Park, South Africa (McGeoch et al. 2002) and snails in Madagascar (Emberton 1996).

It is not possible or advisable to monitor all species; there are simply too many. There are an estimated 10,000 arthropods species in the eastern Sierra alone Sugden (2000). Species level taxonomy and population analyses across the entire arthropod assemblage is inefficient, costly, and poses difficulties in interpretation; use of a small subset of invertebrate taxa as indicators is most effective (Greenslade and New 1991, Kremen et al. 1993, Stork 1994).

Indicator choices based on past success, widespread use, and broad applicability are advisable. Six characteristics that are desirable for insect groups as indicators are outlined by Hellawell (1986) and New (1995):

1) Reasonable, but not overwhelming diversity
2) Well-known taxonomy
3) Easily sampled
4) Sufficient abundance for reliable detection of changes in incidence and abundance
5) Widespread in the target ecosystem
6) A mixture of ecological roles in the taxon and knowledge of these roles

A number of groups have been used with success, such as Diptera and parasitic Hymenoptera (Disney 1986) and ants and termites (Andersen 1990). Ground beetles have been fairly widely used (Stork 1990, Eyre and Luff 1990, Freitag 1979, Pearson and Cassola 1995, New 1995). New (1984, 1987, 1995) suggests multiple indicator groups for terrestrial systems: Collembola (soil and litter, in decomposer food webs), leafhoppers and chrysomelid beetles (herbivores, often host-specific but with different feeding ecologies), ants (particularly valuable because of wide distribution and diverse trophic interactions), and ground beetles (active predators).

There is also information available on groups that have served as poor indicators. Kremen (1992) found butterflies to be good indicators of heterogeneity derived from topographic gradient, but of only limited use for detecting disturbance, and poor indicators of plant assemblage health. Luepke (1979, as per New 1995) also rejected the following taxa as potential indicators: tardigrades (water bears), nematodes, phytophagous insects, hymenopteran parasites, and centipedes. These non-recommendations are based on various factors including small biomass, poor information base, difficulty collecting, and redundancy with other taxa.

Ants have had great success as indicator groups in terrestrial systems (Greenslade 1978, Andersen 1990, Agosti et al. 2000). Much of this utility is due to the following characteristics of ants: extremely abundant, high species richness, many specialists, some species occupy high trophic levels, easily sampled, easily identified, and responsive to changing environmental conditions (Majer 1983). Erhardt and Thomas (1991) found ants to be three times more responsive to environmental change than the plants with which they were associated. Use of functional groups and/or genera of ants can be particularly efficient, because these higher-level groups 1) bypass ignorance of species level biology, 2) simplify complex assemblages, 3) provide insights into major processes, 4) allow meaningful comparisons on a large geographic scale (Andersen 1990).

Based on recent work in subalpine meadows of the Sierra Nevada (Holmquist and Schmidt-Gengenbach 2004, 2005) ant populations, at the generic or perhaps species level, are promising vital signs for monitoring alpine/subalpine meadow health, particularly if combined with monitoring order-level abundances. Per Hellawell's (1986) criteria:

1) Reasonable, but not overwhelming diversity:

    Our collections to date in both the Postpile and Yosemite National Park (Holmquist and Schmidt-Gengenbach 2004) include three subfamilies, seven genera, and ten species (Table 5). Several other species are likely to be collected by an extensive monitoring program, including some invasives.

2) Well-known taxonomy:

    We have excellent species-level keys available, and in addition, RR Snelling will be publishing an additional regional key shortly.

3) Easily sampled:

    Our vacuum apparatus works very well with ants. As seen above, tests with *Formica argentea* yielded a 92% capture rate.

4) Sufficient abundance for reliable detection of changes in incidence and abundance:

   Ants were important constituents of our collections, and these abundances appear to respond to a variety of influences.

5) Widespread in the target ecosystem:

   We collected ants from Yosemite NP (Holmquist and Schmidt-Gengenbach 2004), Devil's Postpile NM (present study), and Sequoia & Kings Canyon NP (ongoing study by Holmquist and Schmidt-Gengenbach), and ants were present in the majority of our samples.

6) A mixture of ecological roles in the taxon; knowledge of these roles:

   Wheeler and Wheeler (1986), and others as cited, provide descriptions of a diversity of foraging habitats, nesting requirements, food sources, and behavioral ecology of the species collected to date (Table 5).

There is an additional benefit to this approach: ants as a group are the most dangerous arthropod invasives (New 1995), and monitoring this taxon would provide early detection of destructive exotic species.

We think that the best cost:benefit relationship for aquatic habitats would be derived from monitoring at the family level. We similarly advocate monitoring terrestrial meadow habitat at the family level for all taxa and additionally tracking ant populations at the genus level. Andersen and Majer (2004) demonstrate that very little signal is lost by monitoring ant genera instead of species.

In addition to minimizing costs via carefully chosen reductions in taxonomic resolution, there are many other cost-saving measures that can be employed to increase replication without significant signal loss. One source of simplification would be to sample only vegetation types that appear to harbor the most fauna: for instance, *Carex utriculata* (Holmquist and Schmidt-Gengenbach 2005). This species would be sampled during both the wet and dry phase. An additional simplification would be to sample only in the first half of the season. Size thresholds for identification of individual specimens can be set, because smaller taxa are much more difficult to process and identify (Andersen and Majer 2004). Some of the terrestrial sorting can be semi-automated via use of Berlese funnels (Bestelmaeyer et al. 2000) or Winkler sacks (Besuchet et al. 1987, Bestelmaeyer et al. 2000), particularly for important indicator taxa such as ants and beetles. Each of these steps could individually reduce costs by as much as 50% and cumulatively could yield an order of magnitude less cost or a ten-fold increase in replication.

Because terrestrial meadow habitat represents a relatively small and accessible component of the Postpile's natural resources, we recommend monitoring these areas in their entirety. We advocate sampling eight randomly-selected plots in both early and mid-season using the vacuum net.

Flooded meadow habitat is even more restricted, appearing during only the first month after snowmelt and representing no more than 30% of the meadows, so sampling throughout these ponded areas would be advisable. We suggest eight random throwtraps during early season.

The reach of the San Joaquin flowing through the Postpile represents a more extensive resource but is manageable enough to be sampled throughout the portion included within NPS boundaries. We recommend the use of three devices: the Surber and habitat samplers used in the present study, plus kick netting with a D-frame net (e.g., Frost et al. 1970, Merritt and Cummins 1996) which does not yield densities but is a good integrative tool. We suggest ten Surber and ten kick net samples allocated evenly throughout the season and randomly distributed spatially. We would add a pair of habitat samplers to be placed annually in selected pools and recovered and processed after one year.

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References

Agosti D, Majer JD, Alonso LE, Schultz TR (eds) (2000) Ants: Standard methods for measuring and monitoring biodiversity, Smithsonian Institution, Washington, DC

Alonso LE (2000) Ants as indicators of diversity. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: Standard methods for measuring and monitoring biodiversity, Smithsonian Institution, Washington, DC, p 80-88

Andersen AN (1990) The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. Proceedings of the Ecological Society of Australia 16:347-357

Andersen AN, Ludwig JA, Lowe LM, Rentz DCF (2001) Grasshopper biodiversity and bioindicators in Australian tropical savannas: Responses to disturbance in Kakadu National Park. Austral Ecology 26:213-222

Andersen AN, Majer JD (2004) Ants show the way down under: invertebrates as bioindicators in land management. Frontiers in Ecology and the Environment 2(6):291-298

Arnold AJ, Needham PH, Stevenson JH (1973) A self-powered portable insect suction sampler and its use to assess the effects of azinphos methyl and endosulfan on blossom beetle populations on oil seed rape. Annals of Applied Biology 75:229-233

Bayfield NG (1979) Recovery of four montane heath communities on Cairngorm, Scotland, from disturbance by trampling. Biological Conservation 15:165-179

Bernstein R (1976) The adaptive value of polymorphism in an alpine ant, *Formica neorufibarbis gelida* Wheeler. Psyche 83:180-184

Bestelmeyer BT, Agosti D, Alonso LE, Brandão CRF, Brown WL Jr, Delabie JHC, Silvestre R (2000) Field techniques for the study of ground-dwelling ants. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: Standard methods for measuring and monitoring biodiversity, Smithsonian Institution, Washington, DC, p 122-144

Besuchet CD, Burckhardt H, Löbl I (1987) The “Winkler/Moczarski” eclector as an efficient extractor for fungus and litter coleoptera. The Coleopterists’ Bulletin 41:392-394

Brostoff WN, Holmquist J, Schmidt-Gengenbach J, Zimba P (submitted) Fairy, tadpole, and clam shrimp (Branchiopoda) in seasonally inundated playas in the western Mojave Desert and effect on primary producers. Hydrobiologia

Brown KS Jr (1997) Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. Journal of Insect Conservation 1:25-42

Buffington ML, Redak RA (1998) A comparison of vacuum sampling versus sweep-netting for arthropod biodiversity measurements in California coastal sage scrub. Journal of Insect Conservation 2:99-106

Callahan RA, Holbrook FR, Shaw FR (1966) A comparison of sweeping and vacuum collecting certain insects affecting forage crops. Journal of Economic Entomology 59:478-479

Chappell HG, Ainsworth JF, Cameron RAD, Redfern M (1971) The effects of trampling on a chalk grassland ecosystem. Journal of Applied Ecology 8:869-882

Cole DN (1995a) Experimental trampling of vegetation. I. Relationship between trampling intensity and vegetation response. Journal of Applied Ecology 32:203-214

Cole DN (1995b) Experimental trampling of vegetation. II. Predictors of resistance and resilience. Journal of Applied Ecology 32:215-224

Clark JA, May RM (2002) Taxonomic bias in conservation research. Science 298:191

Delabie JHC, Fisher BL, Majer JD, Wright IW (2000) Sampling effort and choice of methods. In: Agosti D, Majer JD, Alonso LE, Schultz TR (eds) Ants: Standard methods for measuring and monitoring biodiversity, Smithsonian Institution, Washington, DC, p 145-154

Dethier M (1894) Study on the arthropods associated with an alpine meadow in the Swiss National Park. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 57:317-334

Dietrick EJ, Schlinger EI, Garber MJ (1960) Vacuum cleaner principle applied in sampling insect populations in alfalfa fields by new machine method. California Agriculture 14:9-11

Disney RHL (1986) Assessments using invertebrates: posing the problem. In: Usher MB (ed) Wildlife conservation evaluation. Chapman & Hall, London, P 271-293

Dózsa-Farkas K (1987) Effect of human treading on enchytraeid fauna of hornbeam-oak forests in Hungary. Biology and Fertility of Soils 3:91-93

Eckrich CE, Holmquist JG (2000) Trampling in a seagrass assemblage: direct effects, response of associated fauna, and the role of substrate characteristics. Marine Ecology Progress Series 201:199-209

Elliott JM (1991) Aquatic insects as target organisms for the study of effects of projected climate change in the British Isles. Freshwater Forum 1:195-203

Emberton KC (1996) Conservation priorities for forest-floor invertebrates of the southeastern half of Madagascar: Evidence from two land-snail clades. Biodiversity and Conservation 5:729-741

Erhardt A, Thomas JA (1991) Lepidoptera as indicators of change in the semi-natural grasslands of lowland and upland Europe. In: Collins NM, Thomas JA (eds) The conservation of insects and their habitats. 15th Symposium of the Royal Entomological Society of London. Academic Press, London, p 213-136

Erwin RM, Hafner H, Dugan P (1985) Differences in the feeding behavior of Little Egrets (*Egretta garzetta*) in two habitats in the Camargue, France. The Wilson Bulletin 97:534-538

Eyre MD, Ball SG, Foster GN (1986) An initial classification of the habitats of aquatic Coleoptera in north-east England. Journal of Applied Ecology 23:841-852

Eyre MD, Luff ML (1990) A preliminary classification of European grassland habitats using carabid beetles. In: Stork NE (Ed) The role of ground beetles in ecological and environmental studies. Intercept, Andover, Hants, p 227-236

Eyre MD, Rushton SP (1989) Quantification of conservation criteria using invertebrates. Journal of Applied Ecology 26:159-171

Francoeur A (1973) Révision taxonomique des espèces néarctique du groupe *fusca*, genre *Formica*. Mémoires de la Société Entomologique du Québec 3, 316 pp

Freitag R (1979) Carabid beetles and pollution. In: Erwin TL, Ball GE, Whitehead DR (eds) Carabid beetles: their evolution, natural history and classification. W. Junk, The Hague, p 507-521

Frost S, Huni A, Kershaw WE (1970) Evaluation of a kicking technique for sampling stream bottom fauna. Canadian Journal of Zoology 49:167-173

Greenslade PJM (1978) Ants. In: Low WA (ed) The physical and biological features of Kunnoth Paddock in central Australia. Technical Paper No. 4, CSIRO Division of Land Resources Management

Greenslade P, New TR (1991) Australia: conservation of a continental insect fauna. In: Collins NM, Thomas JA (eds) Conservation of insects and their habitats. Academy Press, London, p 33-70

Gregg RE (1963) The ants of Colorado. University of Colorado Press, Boulder, CO, 792 pp

Hand SC (1986) The capture efficiency of the Dietrick vacuum insect net for aphids on grasses and cereals. Annals of Applied Biology 108:233-241

Harper CA, Guynn DC Jr (1998) A terrestrial vacuum sampler for macroinvertebrates. Wildlife Society Bulletin 26:302-306

Hauer FR, Resh VH (1986) Benthic macroinvertebrates. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology. Academic Press, San Diedo, CA, p 339-369

Hellawell JM (1986) Biological indicators of freshwater pollution and environmental management. Elsevier, London

Henderson IF, Whitaker TM (1977) The efficiency of an insect suction sampler in grassland. Ecological Entomology 2:57-60

Holloway JD (1980) Insect surveys: an approach to environmental monitoring. Atti XII Congresso Nazionale Italiano Entomologica Roma 1:231-261

Holmquist JG (1997) Disturbance and gap formation in a marine benthic mosaic: influence of shifting macroalgal patches on seagrass structure and mobile invertebrates. Marine Ecology Progress Series 158:121-130

Holmquist JG (2004) Terrestrial invertebrates: functional roles in ecosystems and utility as vital signs in the Sierra Nevada. Report submitted to Inventory and Monitoring Program in partial fulfillment of Cooperative Agreement H8R07010001 and Task Agreement J8R07030011.

Holmquist JG, Powell GVN, Sogard SM (1989) Decapod and stomatopod assemblages on a system of seagrass-covered mud banks in Florida Bay. Marine Biology 100:473-483

Holmquist JG, Schmidt-Gengenbach JM (2002) Meadow fragmentation in Yosemite National Park as indicated by invertebrate distributions. Sierra Nevada Science Symposium abstract.

Holmquist JG, Schmidt-Gengenbach JM (2004) User-mediated meadow fragmentation in Yosemite National Park: effects on invertebrate fauna. Final Report to the Yosemite Fund.

Holmquist JG, Schmidt-Gengenbach JM (2005) A pilot study and assessment of the efficacy of invertebrates as indicators of meadow change in Sierra Nevada Network Parks. Interim Report to NPS, Cooperative Agreement H8R07010001.

Hossain Z, Gurr GM, Wratten SD (1999) Capture efficiency of insect natural enemies from tall and short vegetation using vacuum sampling. Annals of Applied Biology 135:463-467

Hower AA Jr, Ferguson W (1972) A square-foot device for use in vacuum sampling alfalfa insects. Journal of Economic Entomology 65:1742-1743

Hughes RD (1955) The influence of the prevailing weather on the numbers of *Meromysa variegata* Meigen (Diptera, Chloropidae) caught with a sweepnet. Journal of Animal Ecology 24:324-335

Jacobsen T, Kushlan JA (1987) Sources of sampling bias in enclosure fish trapping: effects on estimates of density and diversity. Fisheries Research 5:401-412

Jansen A (1997) Terrestrial invertebrate community structure as an indicator of the success of a tropical rainforest restoration project. Restoration Ecology 5:115-124

Jordan F, Jelks HL, Kitchens WM (1994) Habitat use by the fishing spider *Dolomedes triton* in a northern Everglades wetland. Wetlands 14:239-242

Kimsey LS, Cranston P (2002) Final report for the inventory of the insect fauna of Sequoia/Kings Canyon National Parks. University of California, Davis. 16 pp.

Kremen CR (1992) Assessing the indicator properties of species assemblages for natural areas monitoring. Ecological Applications 2:203-217

Kremen C, Colwell RK, Erwin TL, Murphy DD, Noss RF, Sanjayan MA (1993) Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology 7:796-808

Kushlan JA (1981) Sampling characteristics of enclosure fish traps. Transactions of the American Fisheries Society 110:557-562

Leland HV, Fend SV, Carter JL, Mahood AD (1986) Composition and abundance of periphyton and aquatic insects in a Sierra Nevada, California, stream. Great Basin Naturalist 46:595-611

Luepke N-P (ed) (1979) Monitoring environmental materials and specimen banking. Martinus Nijhoff, The Hague

Luff ML, Woiwod IP (1995) Insects as indicators of land use change: a European perspective, focusing on moths and ground beetles. In: Harrington R, Stork NE (eds) Insects in a changing environment. Academic Press, London, p 399-422

Macleod A, Wratten SD, Harwood RWJ (1994) The efficiency of a new lightweight suction sampler for sampling aphids and their predators in arable land. Annals of Applied Biology 124:11-17

Majer JD (1983) Ants: bio-indicators of minesite rehabilitation, land-use and land conservation. Environmental Management 7:375-383

Majer JD (1987) The conservation and study of invertebrates in remnants of native vegetation. In: Saunders DA, Arnold GW, Burbidge AA, Hopkins AJM (eds) Nature conservation: the role of remnants of native vegetation. Surrey Beaty and Sons, London, p 333-335

Mason WT, Anderson JB, and Morrison GE (1967) A limestone-filled artificial substrate sampler-float unit for collecting macroinvertebrates in large streams. *Prog Fish Cult* 29:1-74

McGeoch MA, van Rensburg BJ, Botes A (2002) The verification and application of bio-indicators: a case study of dung beetles in a savanna ecosystem. Journal of Applied Ecology 39:661-672

Merritt RW, Cummins KW, Resh VH (1996) Design of aquatic insect studies: collecting, sampling, and rearing procedures. In: Merritt RW, Cummins KW (eds) An introduction to the aquatic insects of North America, Kendall/Hunt, Iowa, p 12-28

Meyer E (1993) The impact of summer- and winter tourism on the fauna of alpine soils in western Austria (Ötztal Alps, Rätikon). Revue Suisse de Zoologie 100:519-527

Meyer H, Hans-Dieter R (1996) Changes in the biocoenotic structure of the invertebrate fauna of saltmarshes caused by different sheep grazing intensities. Faunistisch-Oekologische Mitteilungen 7:109-151

Minshall GW (1981) Structure and temporal variations of the benthic macroinvertebrate community inhabiting Mink Creek, Idaho, a third order Rocky Mountain stream. Journal of Freshwater Ecology 1:13-26

New TR (1984) Insect conservation: an Australian perspective. W. Junk, Dordrecht

New TR (1987) Insect conservation in Australia: towards rational ecological priorities. In: Majer JD (ed) The role of invertebrates in conservation and biological survey. Department of Conservation and Land Management, Perth, p 5-20

New TR (1993) Angels on a pin: dimensions of the crisis in invertebrate conservation. American Zoologist 33:623-630

New TR (1995) An Introduction to Invertebrate Conservation Biology. Oxford University Press, Oxford, 194 pp

New TR (1998) Invertebrate surveys for conservation. Oxford University Press, Oxford, 240 pp

Oliver I, Beattie AJ (1994) A possible method for the rapid assessment of biodiversity. In: Forey PL, Humphries CJ, Vane-Wright RI (eds) Systematics and conservation evaluation. Clarendon Press, Oxford, UK, p 133-137

Pearson DL, Cassola F (1992) World wide species richness patterns of tiger beetles (Coleoptera: Cicindellidae): indicator taxon for biodiversity and conservation studies. Conservation Biology 6:376-389

Powell W, Walton MP, Jervis MA (1996) Populations and communities. In: Jervis M, Kidd N (eds) Insect natural enemies: practical approaches to their study and evaluation. Chapman and Hall, London, p 223-292

Refseth D (1980) Ecological analysis of carabid communities - potential use in biological classification for nature conservation. Biological Conservation 17:131-141

Richmond CA, Graham HM (1969) Two methods of operating a vacuum sampler to sample populations of the cotton fleahopper on wild hosts. Journal of Economic Entomology 62:525-526

Rosenberg DM, Danks HV, Lehmkuhl DM (1986) Importance of insects in environmental impact assessment. Environmental Management 10:773-783

Rowan DE, Parmenter S (1994) Middle Fork San Joaquin River (Madera County) wild trout management plan. California Department of Fish and Game

Rozas LR, Minello TJ (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries 20:199-213

Ruetz CR III, Trexler JC, Jordan F, Loftus WL, Perry SA (2005) Population dynamics of wetland fishes: spatio-temporal patterns synchronized by hydrological disturbance? Journal of Animal Ecology 74:322-332

Samways MJ (1994) Insect Conservation Biology. Chapman & Hall, London, 358 p

Smith MR (1965) House-infesting ants of the eastern United States. United States Department of Agriculture, Agricultural Research Services Technical Bulletin 1326, 105 pp

Smith DR (1979) Formicoidea. In: Catalog of Hymenoptera in America north of Mexico, vol. 2. Smithsonian Institution, Washington, D.C., p1323-1967

SNEP (1996) Status of the Sierra Nevada. Vol. I. Assessment summaries and management strategies. University of California, Centers for Water and Wildland Resources, Davis. 209 pp.

Stewart AJA, Wright AF (1995) A new inexpensive suction apparatus for sampling arthropods in grassland. Ecological Entomology 20:98-102

Stoneman-Douglas M (1947) The Everglades: river of grass. Pineapple Press, Inc., Sarasota, Florida, 448 pp

Stork NE, (ed) (1990) The role of ground beetles in ecological and environmental studies. Intercept, Andover, Hants

Stork NE (1994) Inventories and biodiversity: more than a question of numbers. In: Forey PL, Humphries CJ, Vane-Wright RI (eds) Systematics and conservation evaluation. Clarendon Press, Oxford, UK, p 81-100

Sugden EA, (2000) Arthropods. In: Smith G (ed) Sierra East: Edge of the Great Basin, Univ. of California Press, Berkeley, CA, p 208-245

Surber EW (1937) Rainbow trout and bottom fauna production in one mile of stream. *Trans Am Fish Soc* 66:193-202

Sutton SL, Collins NM (1991) Insect and tropical forest conservation. In: Collins NM, Thomas JA (eds) Conservation of insects and their habitats. Academy Press, London, p 405-424

Tolbert WW, Tolbert VR, Ambrose RE (1977) Distribution, abundance, and biomass of Colorado alpine tundra arthropods. Arctic and Alpine Research 9:221-234

Uhrin AV, Holmquist JG (2003) Effects of propeller scarring on macrofaunal use of the seagrass *Thalassia testudinum*. Marine Ecology Progress Series 250:61-70

USDI (2001) National Park Service. Biological Inventory Plan for the Sierra Nevada Network. 150 pp.

USDI (2002a) National Park Service. Devils Postpile National Monument Vital Signs Workshop Draft Report. 67 pp.

USDI (2002b) National Park Service. Yosemite Research Symposium Report. 41 pp.

Usher MB (1986) Insect conservation: the relevance of population and community ecology and of biogeography. Proceedings of the Congress of Entomology 3:387-398

Usher MB (1992) Management and diversity of arthropods in Calluna heathland. Biodiversity and Conservation 1:63-79

Whittaker RH (1952) A study of summer foliage insect communities in the great Smoky Mountains. Ecological Monographs 22:1-44

Wheeler GC, Wheeler JN (1986) The Ants of Nevada. Natural History Museum of Los Angeles County, Los Angeles, CA, 138 pp

Yen AL (1987) A preliminary assessment of the correlation between plant, vertebrate, and Coleoptera communities in the Victorian mallee. In: Majer JD (ed) The role of invertebrates in conservation and biological survey. Department of Conservation and Land Management, Perth, Australia, p 73-88

Table 1. River site numbers and UTM coordinates.

1	316050	4166218
2	316186	4164595
3	316158	4163490
4	316220	4165049
5	316064	4166205
6	316107	4166394
7	315995	4165532
8	316018	4165971
9	316125	4164474
10	315926	4163387
11	316186	4165130
12	316100	4164524
13	316199	4164836
14	315907	4163288

Table 2. Arthropod taxa in dry meadow habitat in Devils Postpile National Monument. † = Possible new California record, status currently under review by R. Gill, California Dept of Food & Agriculture.

Insecta

Collembola

Isotomidae
Isotoma?

Odonata

Coenagrionidae
Argia

Orthoptera

Acrididae
Camnula pellucida

Isoptera
Hodotermitidae
Zootermopsis

Hemiptera

Miridae
Labops hesperius?
Labops
Unidentified sp.

Anthocoridae
Xylocoris?

Nabidae
Nabis alternatus?

Lygaeidae

Geocoris

Nysius

Homoptera

Psyllidae

Psylla (Cacopsylla) media

Cicadellidae

Exitianus exitiosus

Amblysellus grex

Dikraneura carneola

Psammotettix lividellus †

Delphacidae

Delphacodes occlusa

Coleoptera

Carabidae

Cicindela oregona?

Notaphus

Laemostenus complanatus?

Staphylinidae

Homalota?

Doliponta?

Tachyporus

Scarabaeidae

Serica

Buprestidae

Sphaerobothris

Elateridae

Horistonotus

Coccinellidae

Unidentified larva

Anthicidae

Ischyropalpus?

Chrysomellidae

Metachroma?

Curculionidae

Unidentified

Hymenoptera

Tenthredinidae

Unidentified sp.

Subf. Nematinae (larva)

Ichneumonidae

Unidentified sp.

Chrysididae

Chrysis pacifica

Pteromalidae

Unidentified sp.

Platygastridae

Unidentified sp.

Formicidae

Camponotus modoc

Formica hewitti

Formica neorufibarbis

Formica fusca

Myrmica sp.1

Sphecidae

Chlorion?

Lepidoptera

Lycaenidae
Glaucopsyche piasus

Diptera

Chironomidae
Polypedilum
Unidentified

Culicidae
Aedes hexadontus
Aedes cataphylla

Bibionidae
Bibio

Tabanidae
Chrysops

Simuliidae
Simulium

Bombiliidae
Anthrax

Empididae
Unidentified

Lonchopteridae
Lonchoptera furcata?

Phoridae
Megasilea?
Plastophora?

Anthomyiidae
Botanophila?
Chirosia?

Muscidae

Fannia
Musca?
Thricops?

Sarcophagidae

Boettcheria

Agromyzidae

Amauromyza?
Agromyza sp. 1
Agromyza sp. 2

Opomyzidae

Geomyza

Chloropidae

Chlorops?
Homaluroides?
Siphonella?
Meromyza pratorum

Sphaeroceridae

Halidayina?

Araneae

Theridiidae

Theridion murarium?

Linyphiidae

Unidentified sp. 1
Unidentified sp. 2

Dictynidae

Dictyna reticulata

Lycosidae

Pardosa

Philodromidae
Philodromus

Salticidae
Habrocestum

.

Table 3. Arthropod taxa in flooded meadow habitat in Devils Postpile National Monument.

Insecta

Ephemeroptera

Siphlonuridae
Siphlonurus sp. 1

Odonata

Coenagrionidae
Argia

Hemiptera

Gerridae
Gerris remigis

Saldidae
Saldula

Belostomatidae
Lethoceris americanus

Trichoptera

Limnephilidae
Lenarchus rillus?

Diptera

Tipulidae
Gonomyia

Culicidae

Aedes hexadontus
Aedes ventrovittis
Aedes cataphylla
Aedes melanimon
Aedes increpitus

Bibionidae

Bibio

Stratiomyidae

Caloparyphus sp. 1
Caloparyphus sp. 2

Tabanidae

Chrysops

Coleoptera

Gyrinidae

Gyrinus

Dytiscidae

Hydroporus axillaris?
Hydroporus subpubescens?
Hydroporus sp. 1
Rhantus
Hydaticus
Agabus
Laccophilus decipiens

Hydrophilidae

Helophorus
Hydrobius fuscipes?
Hydrobius sp.

Hydraenidae

Hydraena vandykei?
Ochthebius holmbergi?

Table 4. Arthropod taxa from the San Joaquin River in Devils Postpile National Monument. *= new record for the Postpile.

Insecta

Ephemeroptera

Ephemerellidae
Drunella doddsi
Drunella flavilinea
Drunella sp.
Serratella sp.1
Serratella sp.2*
Caudatella hystrix?
*Ephemerella**

Heptageniidae
Cinygmula
Epeorus sp. 1
Epeorus sp. 2
Rithrogena

Ameletidae
Ameletus sp.

Leptophlebiidae
*Paraleptophlebia **

Baetidae
Baetis sp. 1
Baetis sp. 2

Trichoptera

Glossosomatidae*
*Agapetus * taho?*

Polycentropodidae*
*Polycentropus**

Brachycentridae

Brachycentrus * *americanus?*

Micrasema

Philopomatidae

Dolophilodes *

Hydropsychidae*

Hydropsyche *

*Arctopsyche** *grandis?*

Limnephilidae

Unidentified pupa

Uenoidae*

*Oligophlebodes** *sierra*?

Hemiptera*

Saldidae*

Unidentified early instar

Plecoptera

Perlidae

Hesperoperla *

Pteronarcyidae

Pteronarcys

Chloroperlidae

Suwallia

Leuctridae*

*Paraleuctra**

Perlodidae*

*Perlinodes**

Nemouridae
Malenka

Peltoperlidae
Yoroperla

Diptera

Chironomidae
Orthocladiinae sp.1
Orthocladiinae sp.2
Polypedilum
Thienemannimyia group
Eukiefferiella
Microspectra or *Tanytarsus*

Tipulidae
Hexatoma *
Dichronota *
Antocha monticola?
*Limnophila**

Psychodidae*
*Pericoma**

Simuliidae
Simulium

Athericidae
Atherix

Empididae
Unidentified

Coleoptera

Elmidae

Cleptelmis *

Narpus

Ampumixis?*

Zaitzevia parvula?

Optioservus quadrimaculatus

Table 5, continued next page. Ant taxa collected in Devils Postpile National Monument (current study) and/or Yosemite National Park (Holmquist and Schmidt-Gengenbach 2004) illustrating diversity of foraging habitats, nesting requirements, food sources, and behavioral ecology (largely derived from Wheeler and Wheeler 1986).

Family Formicidae

Subfamily Formicinae

Camponotus modoc

Workers highly polymorphic, live in forest-dominated habitats in stumps, fallen trees, in heartwood of injured trees that are still standing, and soil. Eat dead and living insects, plants (sap and other secretions), seeds, fruit, pollen, nectar, fungi, honey, honeydew, do not eat wood removed from their galleries.

Formica fusca

High altitude. Nests under stones and occasionally under wood or in exposed soil. Fast-moving, timid. Sometimes enslaved by other species.

Formica hewitti

Mid- to high altitude. Nests under stones, among plant roots, and in fallen trees.

Formica neorufibarbis

Lives at high altitude; holds elevational record for Nearctic ant fauna (Gregg 1963). Generally docile. Brood reared quickly (adaptation to short summer). Feeds on honeydew, liquid from plants (mostly flowers), and dead arthropods (Francoeur 1973, Bernstein 1976).

Formica subpolita

Mid- to high altitude. Nests under stones or exposed soil. Fast-moving, timid. Sometimes tends mealybugs (Homoptera).

Subfamily Dolichoderinae

Conomyrma insana
Nests in exposed soil. Predaceous but feed on honeydew when available. Forages in rapidly-moving files

Tapinoma sessile
Most common in forest-dominated areas. Common, wide-ranging, versatile, variety of habitats. Lives in soil under stones and other objects, under loose bark of stumps and logs, and in plant cavities. Workers do not exhibit the usual intraspecific hostility between colonies. Feed on secretions of floral nectaries, dead & living insects, sometimes cultivate aphids for honeydew.

Subfamily Myrmicinae

Solenopsis validiuscula
Monomorphic. Most common & widespread thief ant, nesting in walls separating chambers in nests of larger species, where this species robs food and brooded larvae; sometimes nests under stones, rotting wood, or exposed soil. Omnivorous or predaceous, feeds on dead & live insects, can be highly granivorous also, workers known to tend mealybugs, plant lice, scale insects (Smith 1965).

Leptothorax crassipilis
Form small colonies in rotten wood, soil, insect galls, and nests of other species, with a preference for pre-formed cavities.

Myrmica brevispinosa group
Montane genus. Prefers damp localities. Nests chiefly under stones, can be in soil or rotten wood. Workers carnivorous, but also feed on honeydew of Homoptera and exudates of plants (Smith 1979).

Figure Captions

Fig 1. Clockwise from upper left: winter, early, mid, and late season meadow habitat from approximately the same vantage point. Circle in winter photo indicates a 10 cm exposure of the 2.5 m tall willow stand seen in the early season photo; the rest of the stand is under the snow. Note flooding and persisting snow in early season.

Fig 2. Devils Postpile, indicating meadow sites on either side of the San Joaquin River (open circles) and Surber sampling locations in the river (diamonds).

Fig 3. Tossing the throw trap into flooded meadow habitat.

Fig 4. Clockwise from upper left: scooping fauna out of the throw trap, washing the bar seine, sorting fauna from detritus, and using the plankton splitter to split samples into equal portions.

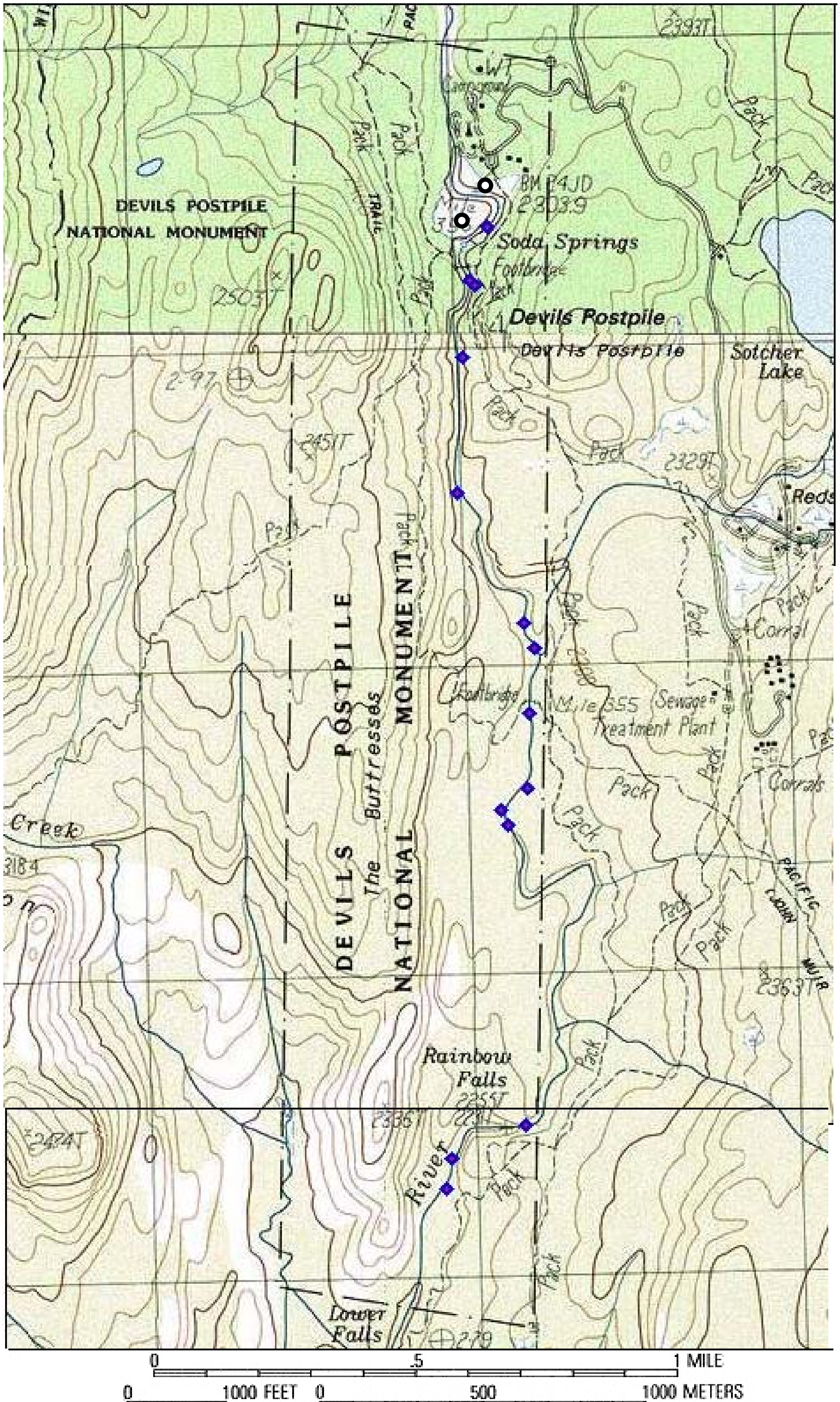
Fig 5. Tossing the netted quadrat and vacuuming fauna from vegetation through the elasticized aperture in the net. L. Greene photos.

Fig 6. Surber sampling.

Fig 7. Substrate sampler location one year after placement. A portion of the upper basket, underscored by the white line, is barely emergent from the substrate.


Fig 1

Fig 2


DEVILS POSTPILE
NATIONAL MONUMENT
Soda Springs
Footbridge
Devils Postpile
Devils Postpile
Sotcher Lake
BM 24JD
2303.9
2503T
2451T
2329T
DEVILS POSTPILE NATIONAL MONUMENT
The Buttresses
Footbridge
Mile 355
Sewage Treatment Plant
Corral
Corrals
Creek
PACIFIC CREST
2363T
Rainbow Falls
2255T
2336T
2474T
River
Lower Falls
0
.5
1 MILE
0
1000 FEET
0
500
1000 METERS

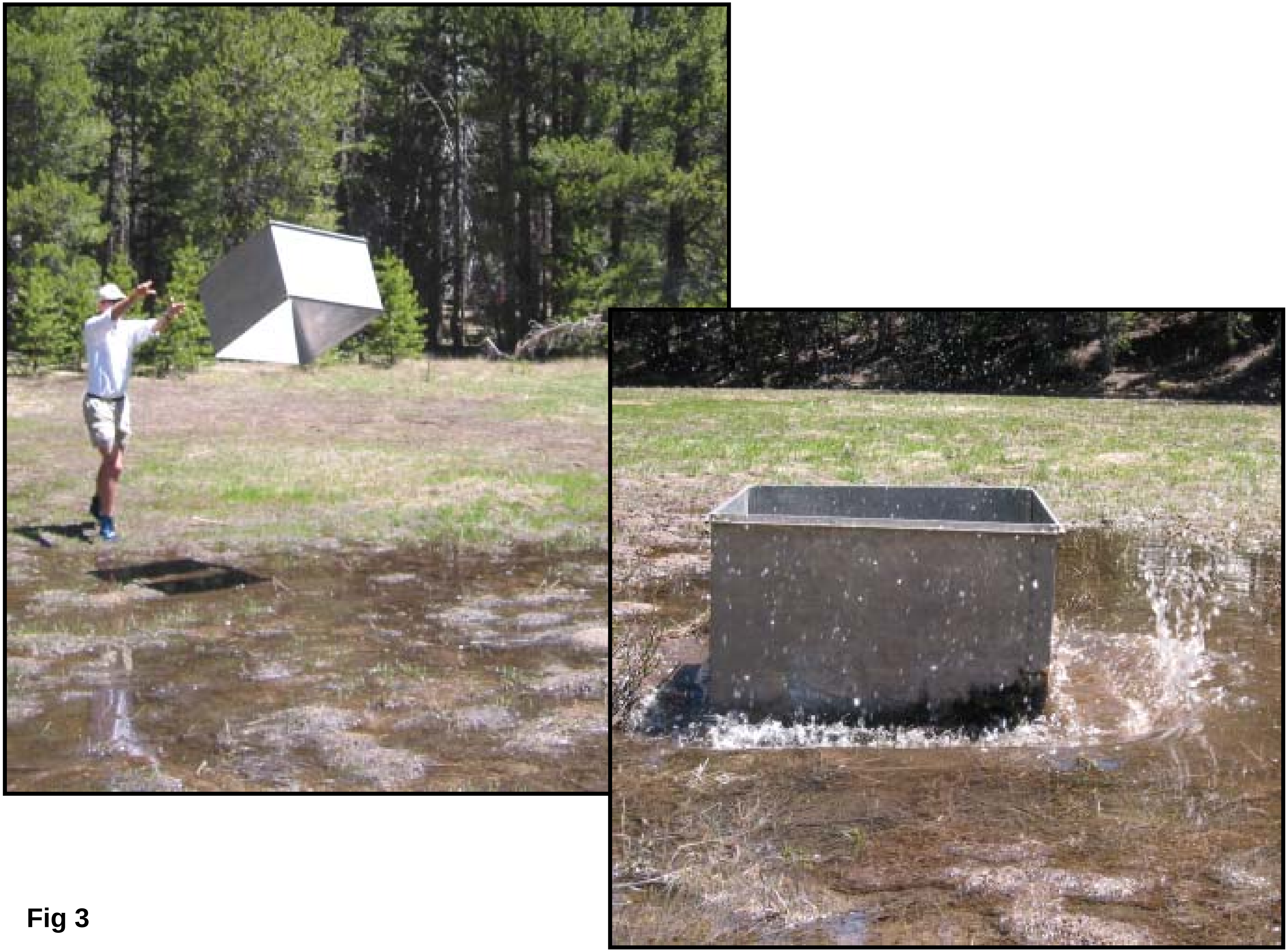


Fig 3

Fig 4

P. Moore

Fig 5


Fig 6
Flow

Fig 7

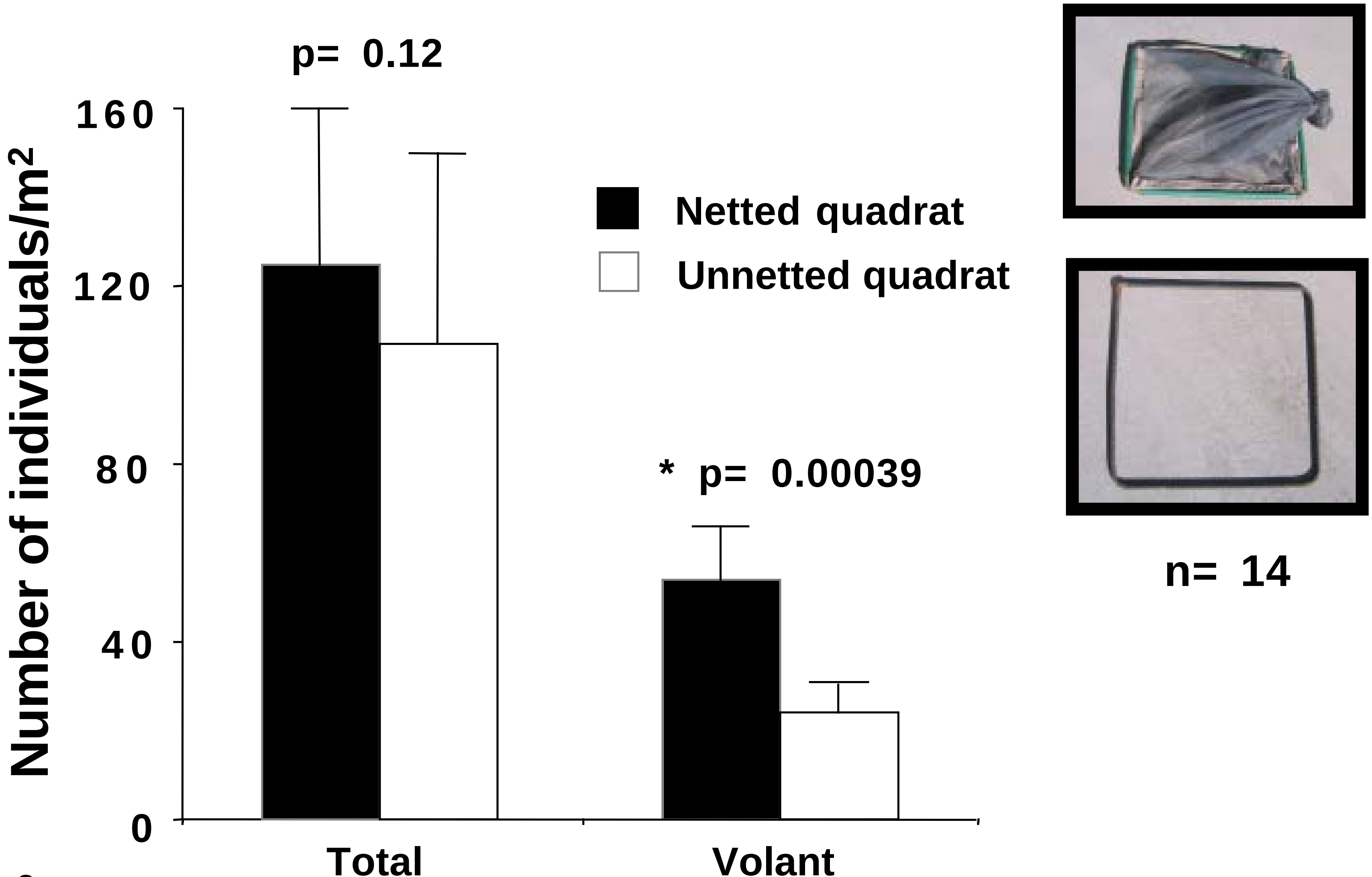

p= 0.12
160
120
80
40
0
Number of individuals/m²
Netted quadrat
Unnetted quadrat
* p= 0.00039
Total
Volant
n= 14

Fig 8

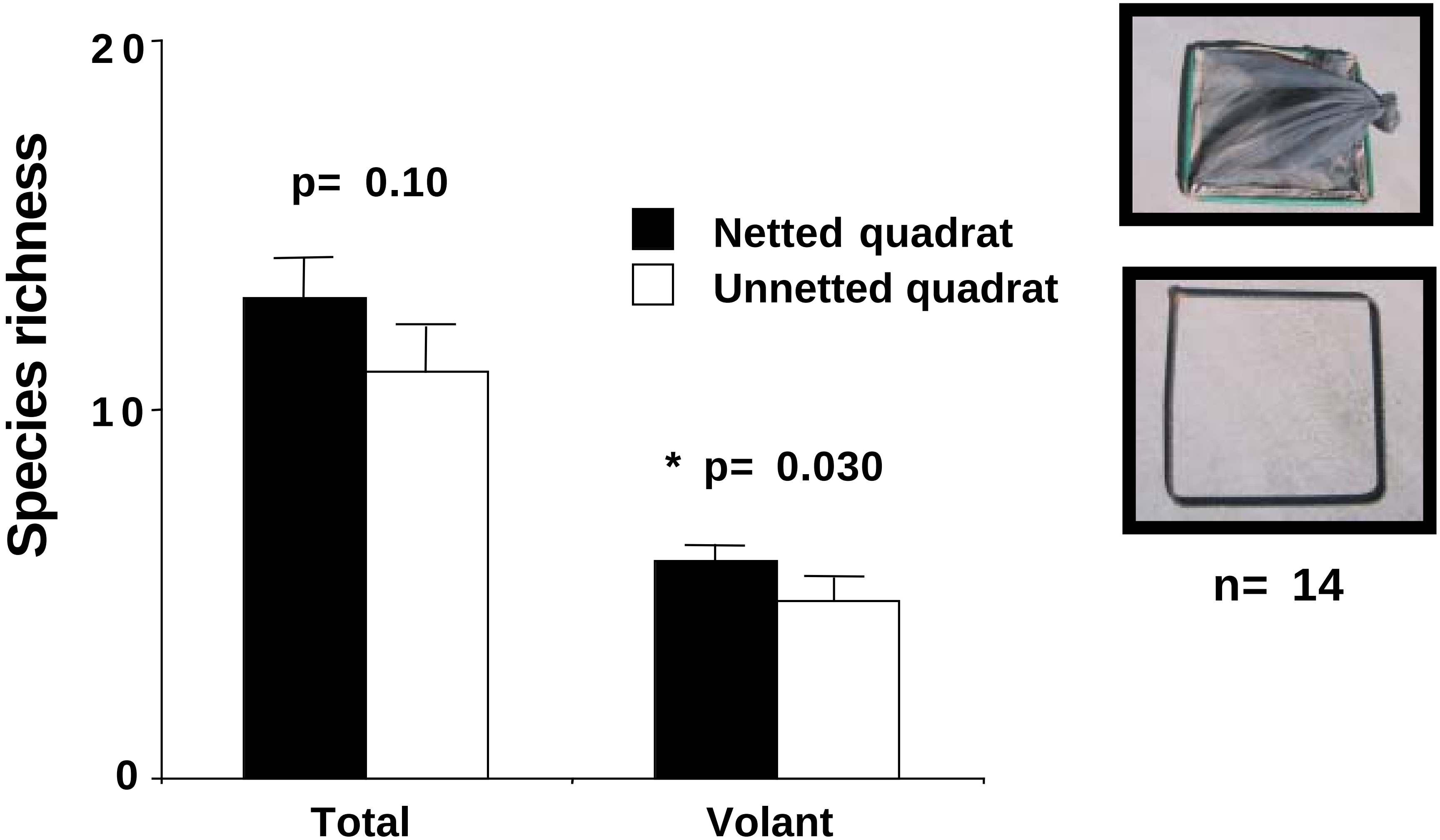

2 0
1 0
0
Species richness
p= 0.10
* p= 0.030
Netted quadrat
Unnetted quadrat
Total
Volant
n= 14

Fig 9

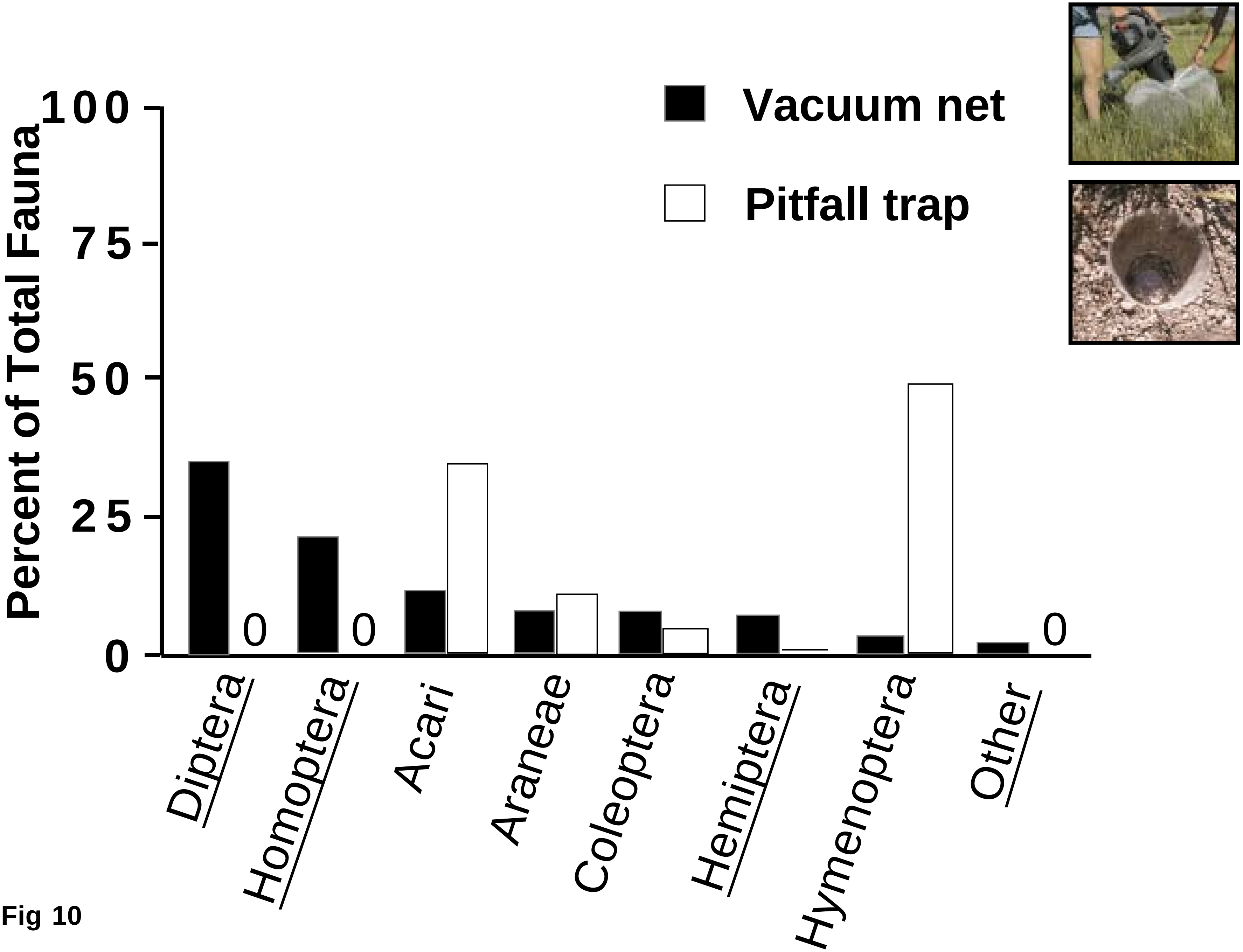
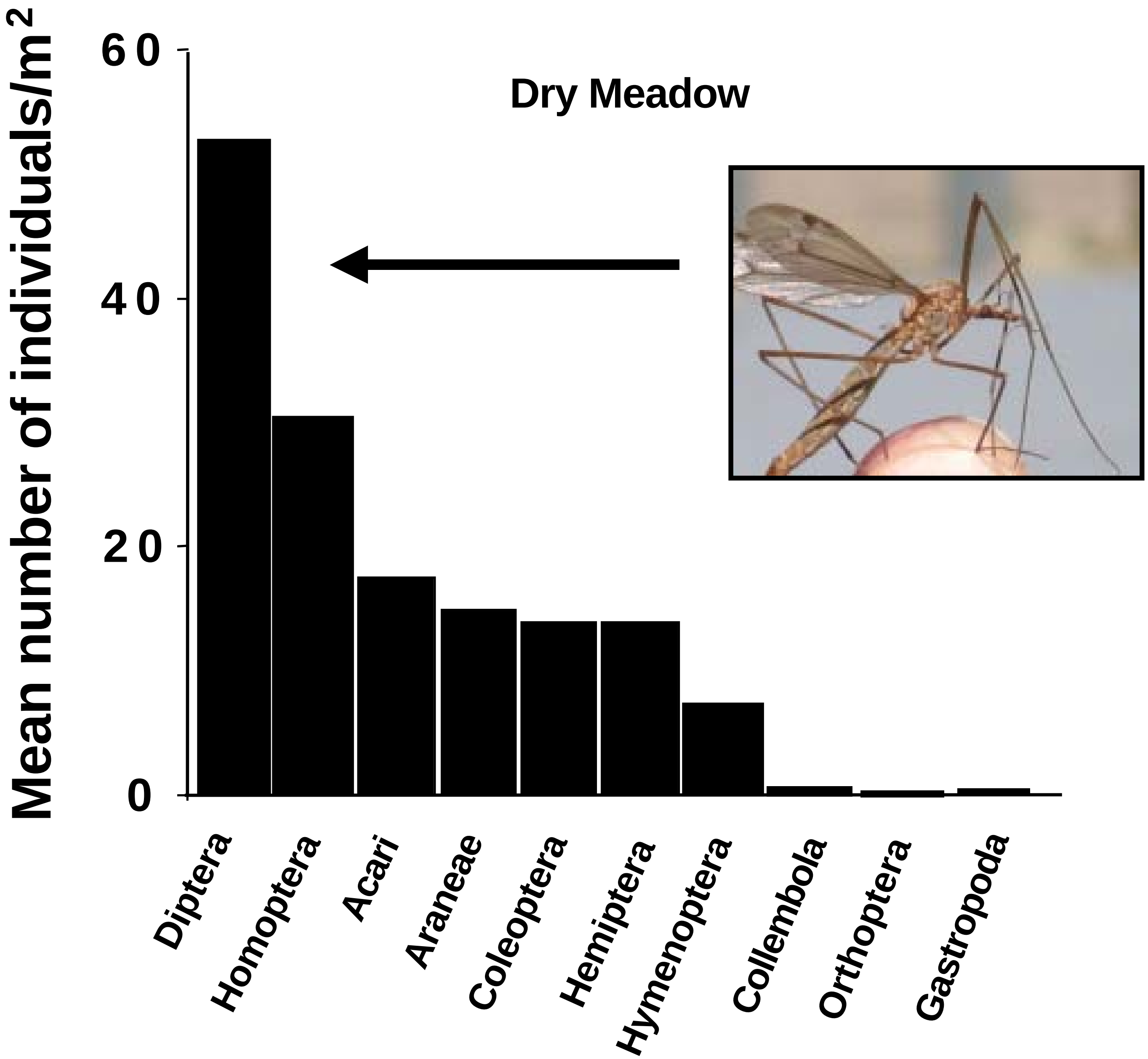

Vacuum net
Pitfall trap
Percent of Total Fauna
100
75
50
25
0
0
0
0
Diptera
Homoptera
Acari
Araneae
Coleoptera
Hemiptera
Hymenoptera
Other

Fig 10



Dry Meadow
Mean number of individuals/m²
60
40
20
0
Diptera
Homoptera
Acari
Araneae
Coleoptera
Hemiptera
Hymenoptera
Collembola
Orthoptera
Gastropoda

Fig 11

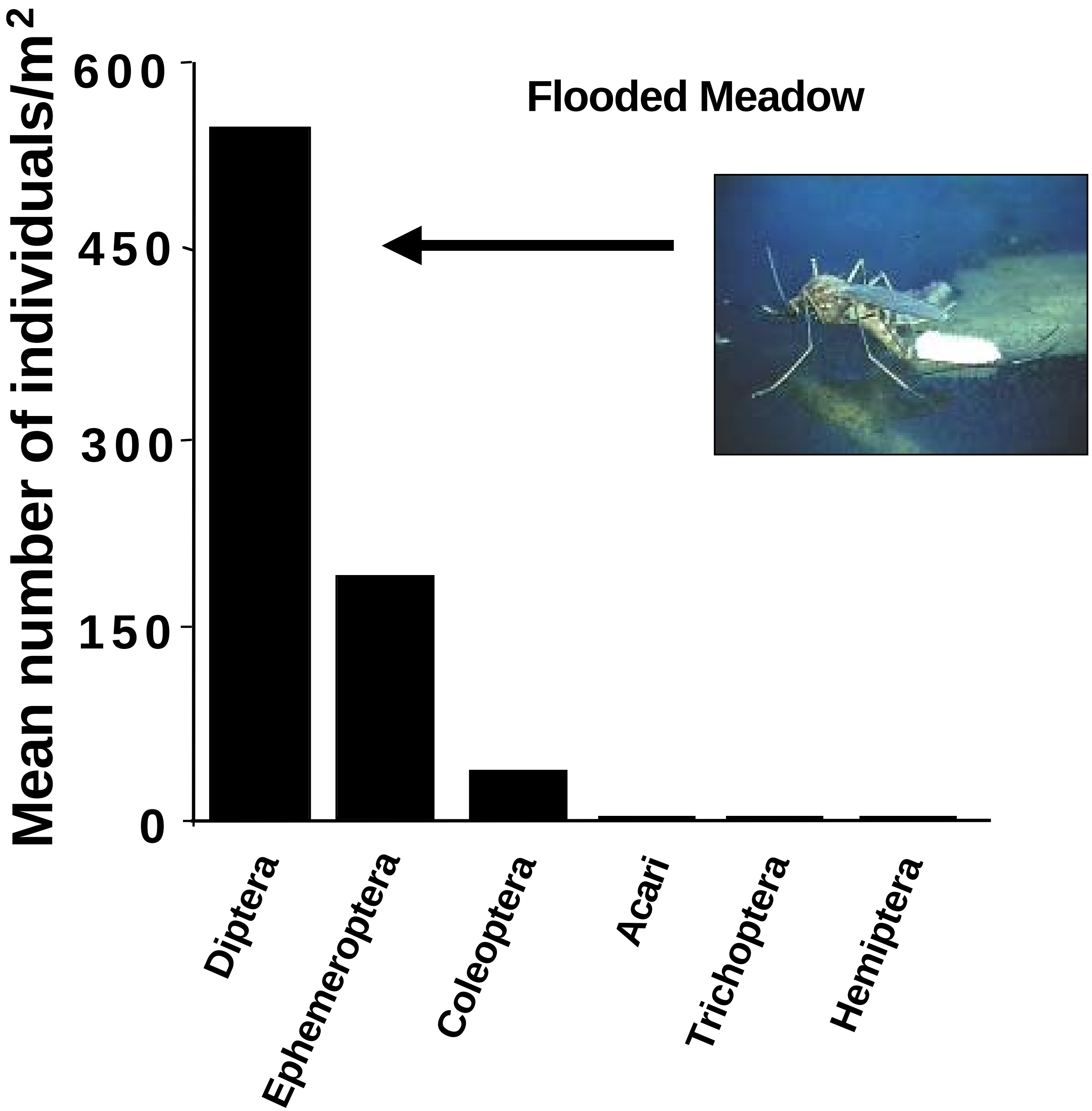
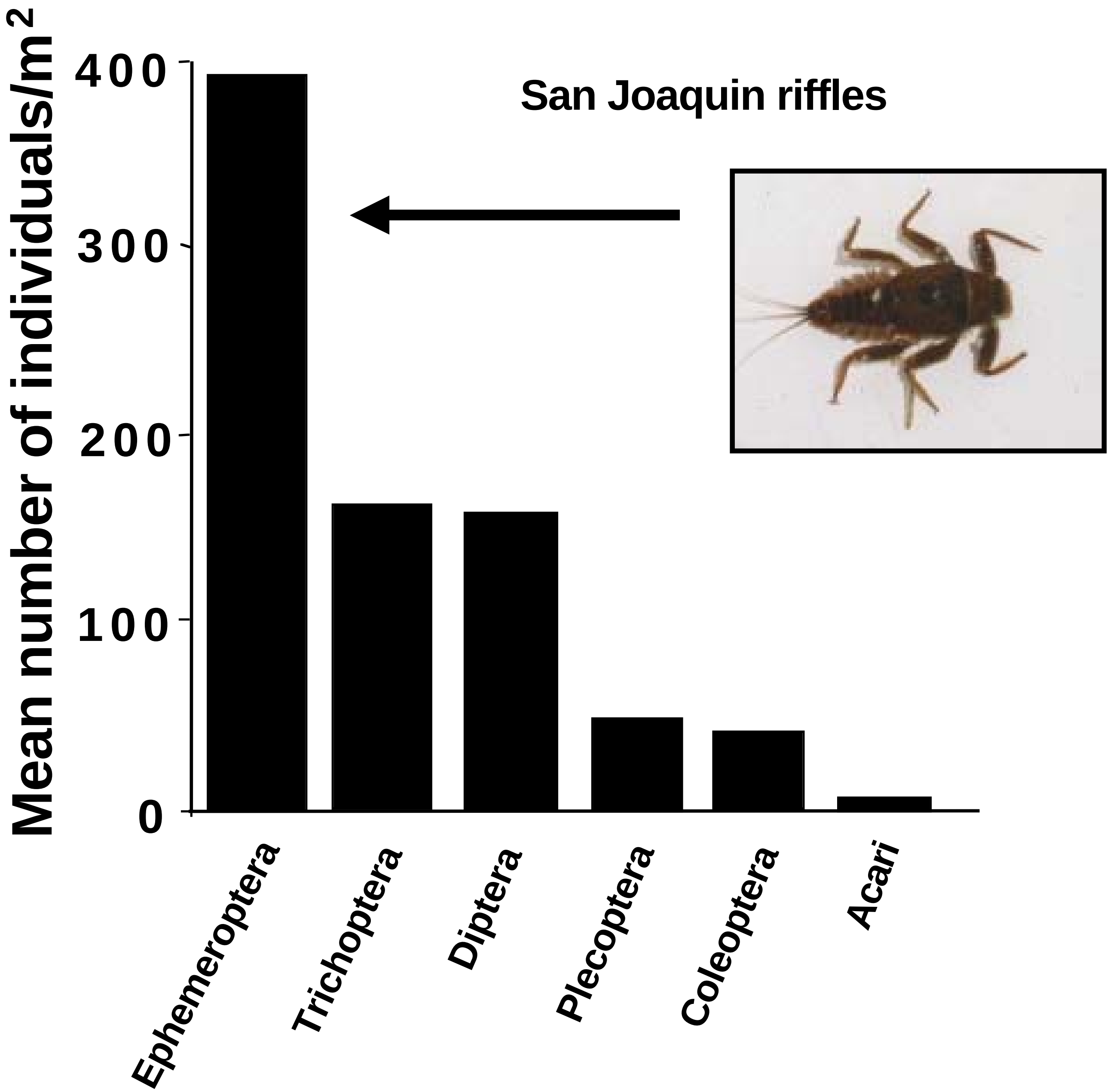
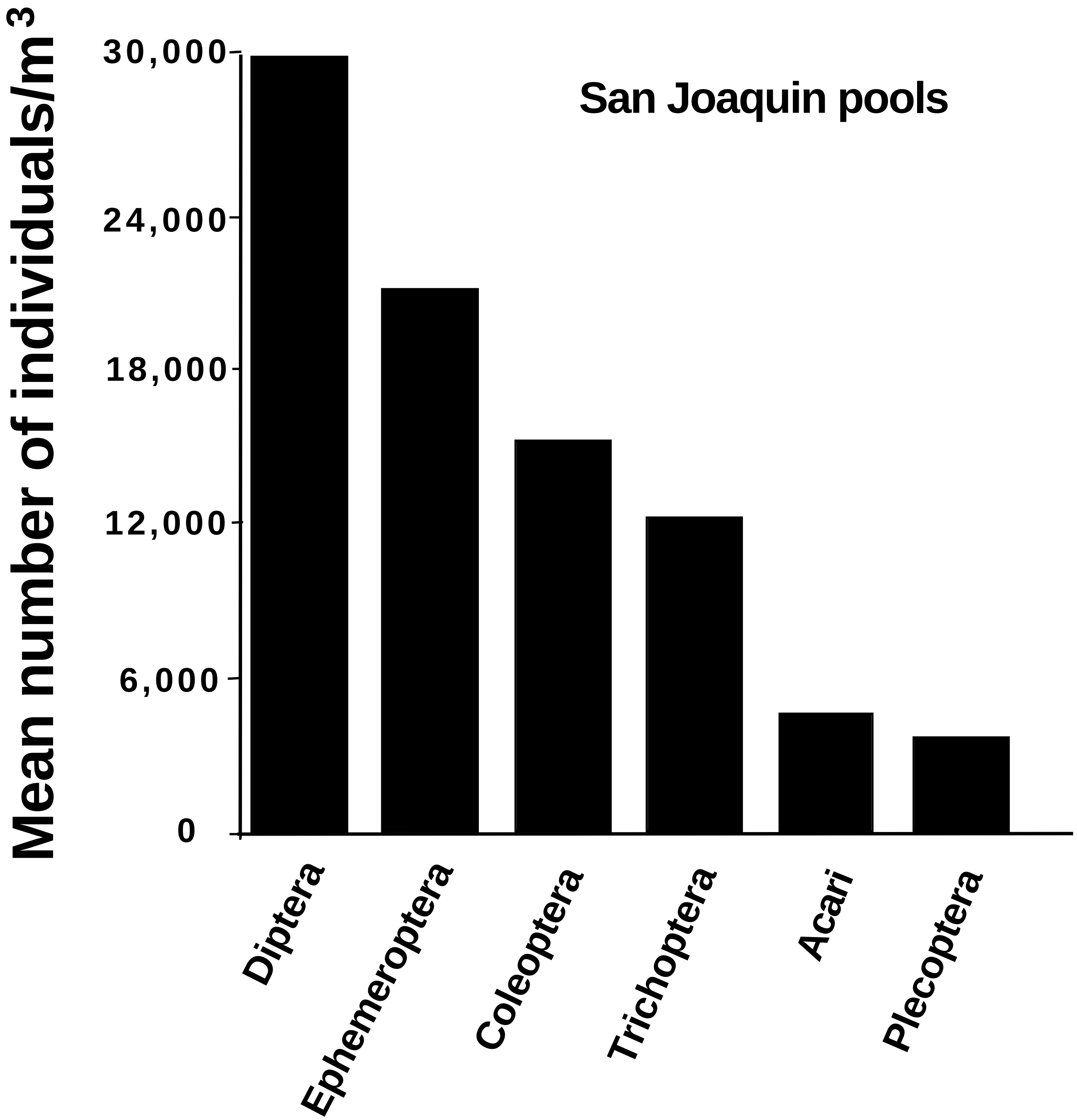

Mean number of individuals/m^2
600
450
300
150
0
Flooded Meadow
Diptera
Ephemeroptera
Coleoptera
Acari
Trichoptera
Hemiptera

Fig 12



San Joaquin riffles
Mean number of individuals/m2
400
300
200
100
0
Ephemeroptera
Trichoptera
Diptera
Plecoptera
Coleoptera
Acari

Fig 13



San Joaquin pools
Mean number of individuals/m³
30,000
24,000
18,000
12,000
6,000
0
Diptera
Ephemeroptera
Coleoptera
Trichoptera
Acari
Plecoptera

Fig 14

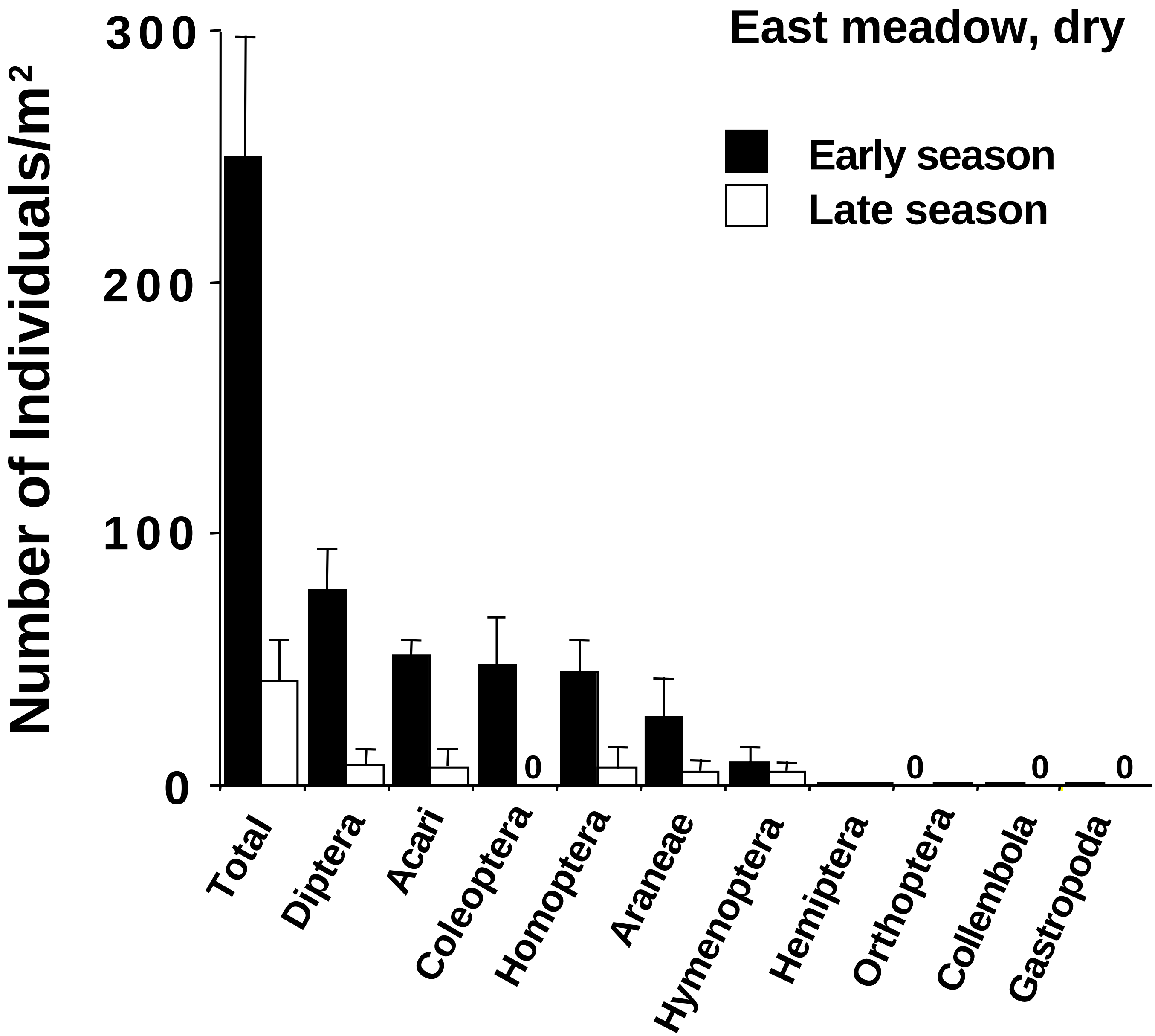

East meadow, dry
Early season
Late season
Number of Individuals/m2
300
200
100
0
Total
Diptera
Acari
Coleoptera
Homoptera
Araneae
Hymenoptera
Hemiptera
Orthoptera
Collembola
Gastropoda

Fig 15

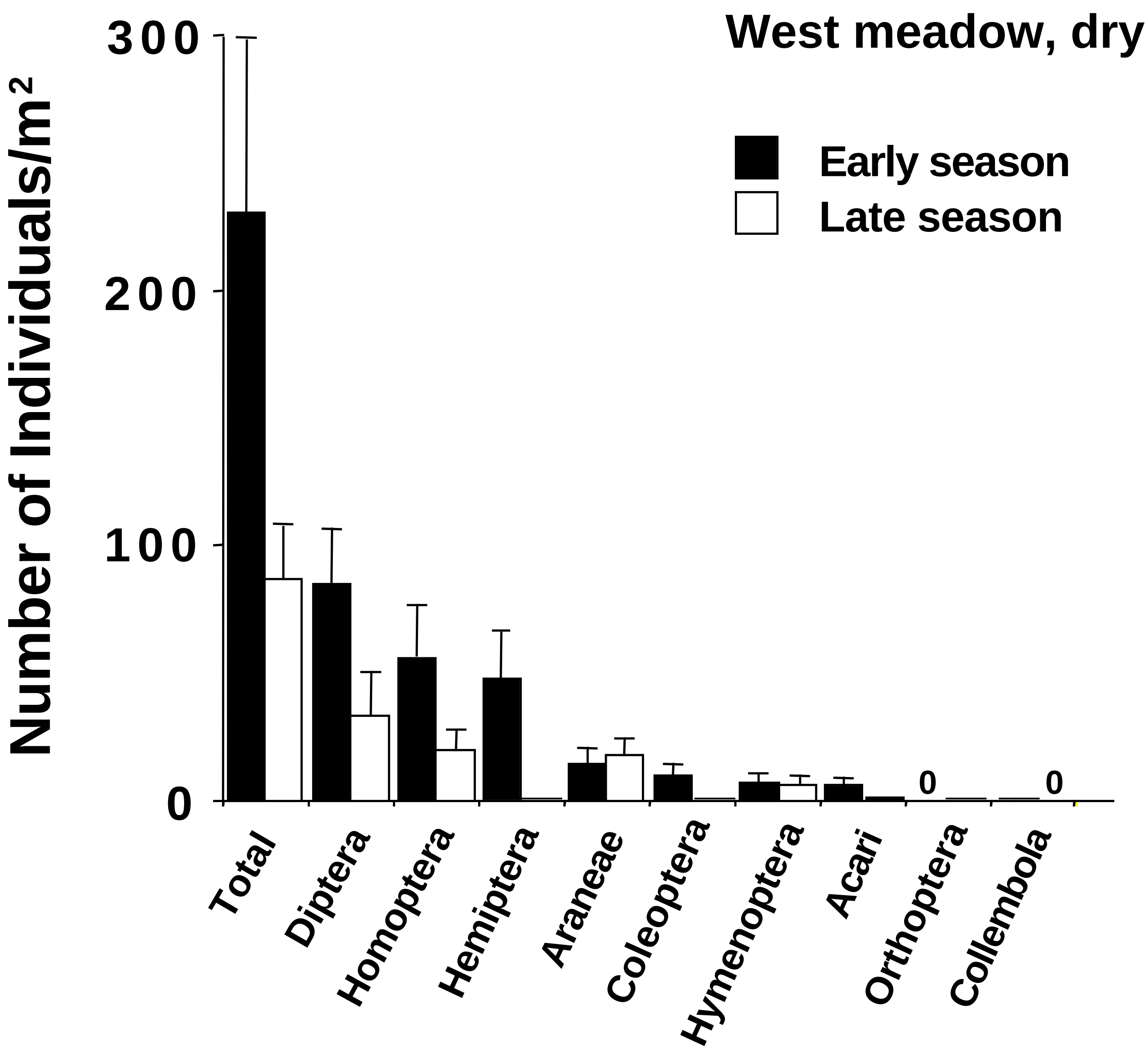

West meadow, dry
Early season
Late season
Number of Individuals/m²
300
200
100
0
0
0
Total
Diptera
Homoptera
Hemiptera
Araneae
Coleoptera
Hymenoptera
Acari
Orthoptera
Collembola

Fig 16

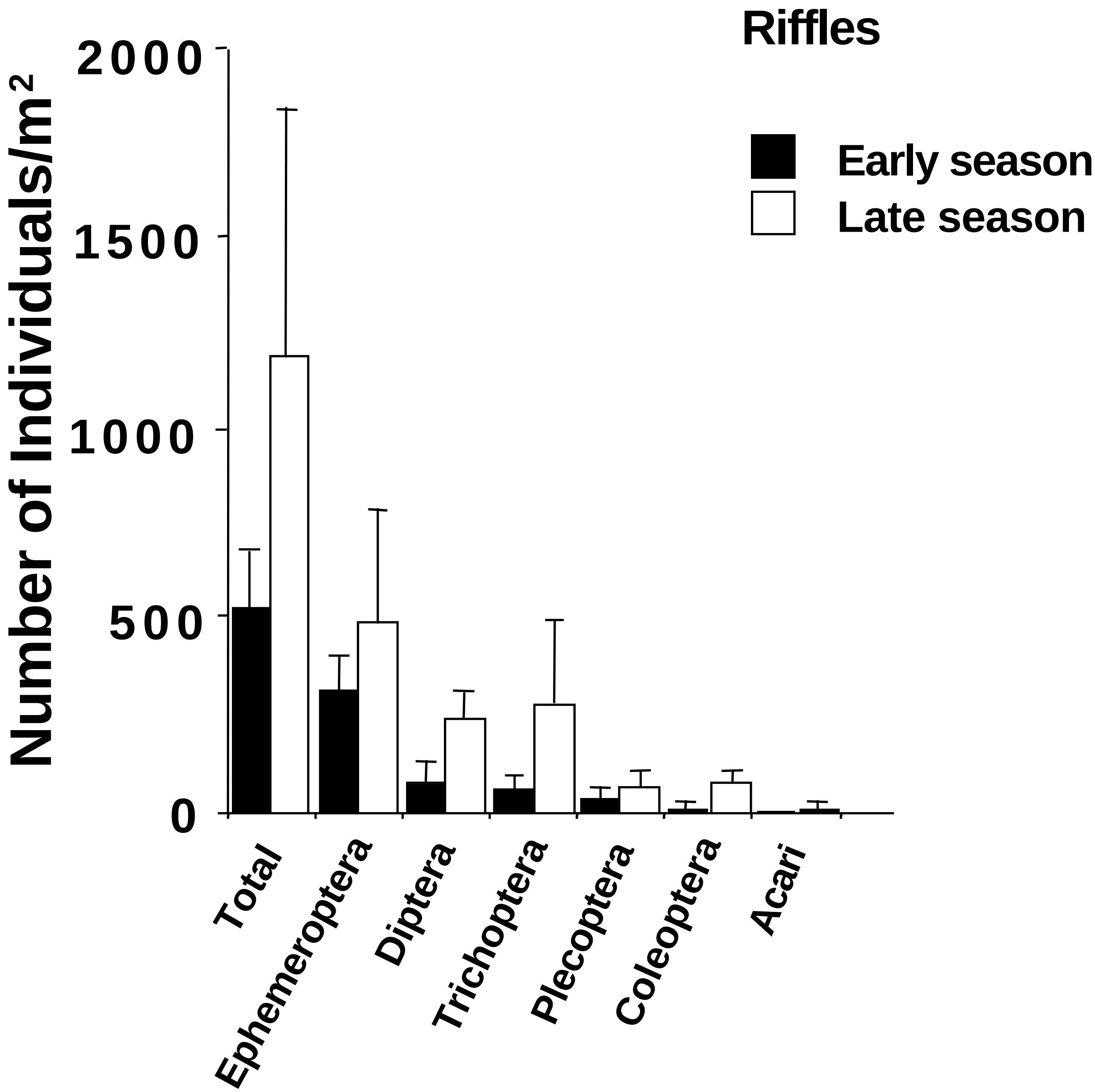
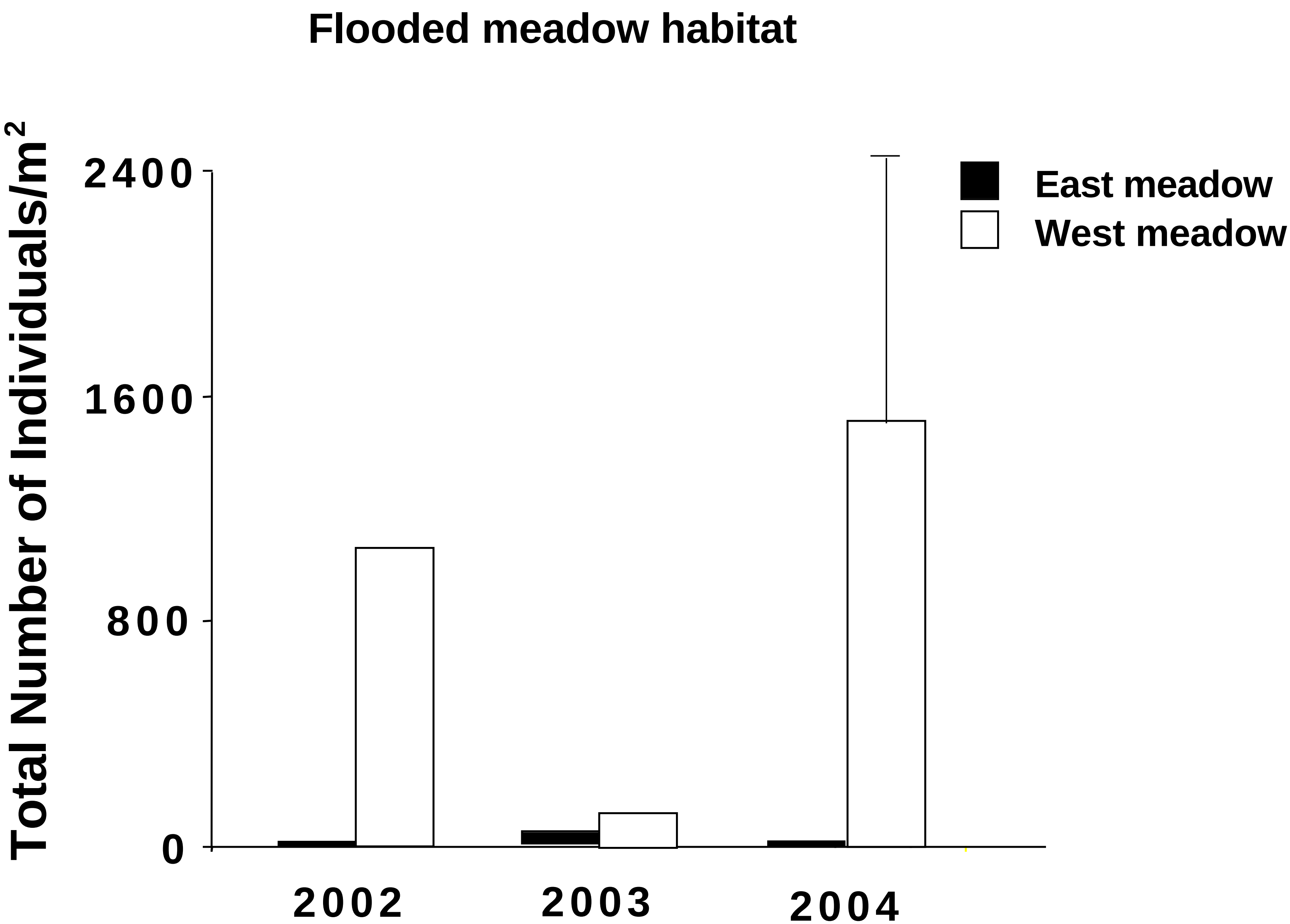

Riffles
Early season
Late season
Number of Individuals/m2
2000
1500
1000
500
0
Total
Ephemeroptera
Diptera
Trichoptera
Plecoptera
Coleoptera
Acari

Fig 17



Flooded meadow habitat
Total Number of Individuals/m^2
2400
1600
800
0
East meadow
West meadow
2002
2003
2004

Fig 18

Dry meadow habitat

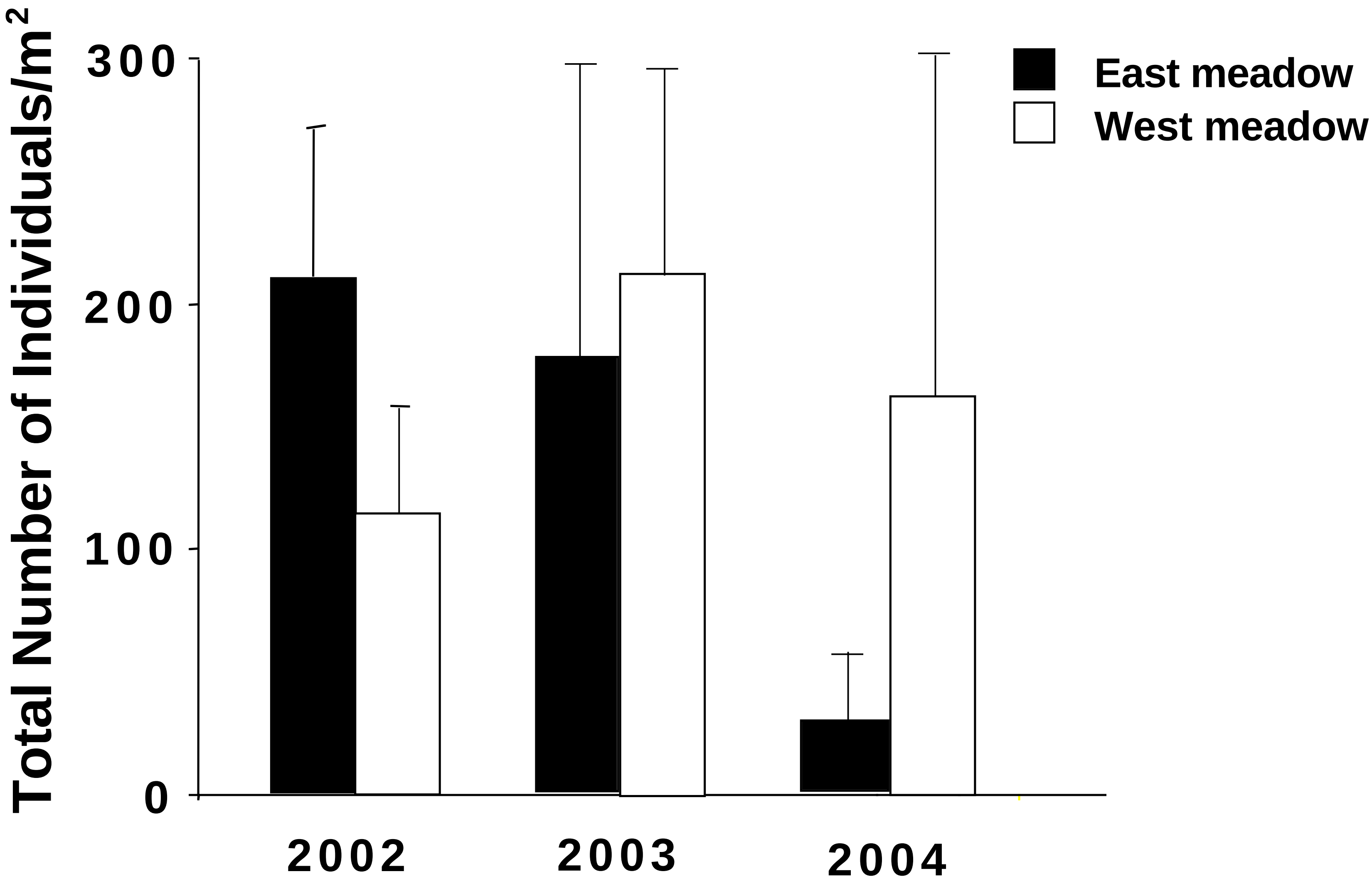


Fig 19